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THE GROWTH AND BREEDING OF THE MULTIMAMMATE RAT, *RATTUS* (*MASTOMYS*) *NATALENSIS* (SMITH) IN TANGANYIKA TERRITORY

BY

B. M. CHAPMAN AND R. F. CHAPMAN

Biological Research Institute, University College of Ghana, Achimota, Ghana

AND

I. A. D. ROBERTSON

Ukiruguru Research Station, P.O. Fela, Lake Province, Tanganyika

[Accepted 14th October 1958]

(With 6 figures in the text)

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INTRODUCTION

While the authors were living in the Rukwa Valley, Tanganyika Territory, plagues of the Multimammate Rat, *Rattus natalensis*, occurred. The following data on their growth and breeding were collected during the period February, 1955 to February, 1957, mainly in the central area of the valley.

HABITAT

Rattus natalensis was common in and near houses in the narrow belt of forest which bordered the extensive grass plains of the valley floor. The forest was characterized by *Acacia*, *Sterculia* and *Commiphora* spp., among other trees, in open canopy and, during the wet season, the ground between the trees was covered by tall grasses, *Panicum maximum*, *Digitaria milanjiana* and *Hyparrhenia gracilescens* being the dominant species. During the dry season this grass was burnt off so that the ground was virtually without cover from July to November. *R. natalensis* was not found out on the grass plains. This may have been related to a similar restriction of the human population to the fringing forest since Pirlot (1953) only found this species within 500 m. of human dwellings and remarks that it is known to be a human commensal.

SEASONAL ABUNDANCE

Large fluctuations in the sizes of *R. natalensis* populations are known to occur and plagues in Tanganyika during 1955–56 have been reported (Tanganyika, 1957). Systematic trapping methods were not used in this study so

that no information on population dynamics was obtained. However, the seasonal variation in the number of rats collected was so marked that the broad outlines of the changes in population were readily apparent. The collector was told to catch a minimum of twenty rats each month and although in some months over 300 were obtained in others he was unable to catch the required number. Fig. 1 shows the number of rats dissected each month ;

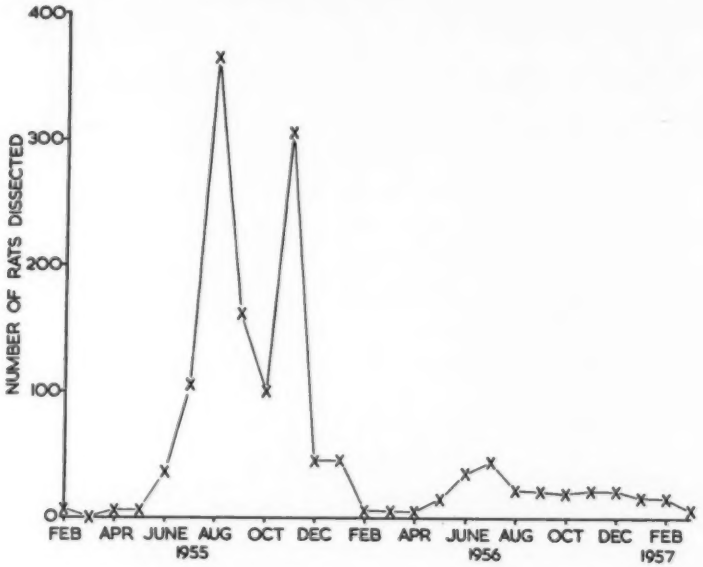

Fig. 1.—The number of *Rattus natalensis* dissected each month during the observations. This gives an indication of the seasonal fluctuations in numbers.

more than twenty were examined each month from June to December, 1955 and again from June to November, 1956 but for the remainder of the period only very small numbers were obtained.

Independent evidence of this seasonal variation in numbers was obtained from the numbers of rats caught in open, unbaited petrol drums sunk into the floor in grain stores belonging to the International Red Locust Control Service (Table 1). Trapping first became necessary in Milepa store in August, 1955. Nearly all the rats caught were *R. natalensis* but there were also a few *R. rattus*. The number caught fell off throughout the remainder of the year, due at least in part to the trapping, until very few were taken in December. At Muse, some 45 miles to the north of Milepa, no trapping was necessary in 1955 or until July, 1956. Large numbers were caught up to November but after this trapping was discontinued because the catches were relatively small.

From this evidence it appears that *R. natalensis* was very common from June to November or December but relatively scarce from January to May,

TABLE 1

The numbers of rats caught in drums in grain stores in 1955 and 1956

	1955 (Milepa Camp)		1956 (Muse Camp)	
	No. days catching	Av. catch per day	No. days catching	Av. catch per day
July	0	—	17	1398
August	8	153	31	1046
September	30	35	30	655
October	31	45	31	82
November	30	33	8	36
December	31	19	0	—

which roughly corresponds to the rainy season. Pirlot & van den Bulcke (1952) recorded comparable seasonal fluctuations in the Belgian Congo, larger numbers being collected in the dry seasons.

MORPHOMETRICS AND MATURATION

All the rats collected were measured ; body length was taken as the distance from the tip of the snout to the anus, tail length as the distance from the anus to the tip of the tail. A suitable balance became available in October, 1955 and from then onwards the rats were weighed as soon after killing as possible. Fig. 2 shows the increase of weight with length. Young males and females were similar in weight for a given body length, the mean weight increasing

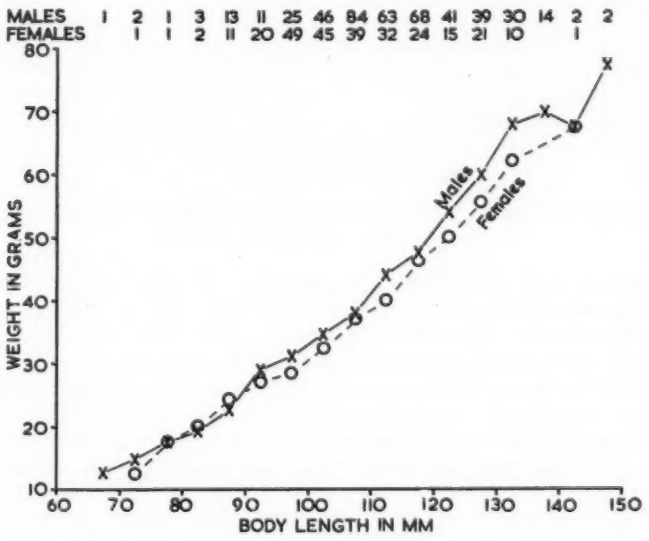

Fig. 2.—Weight relative to length of male and female rats. The numbers at the top of this and Fig. 5 show the number of rats on which each point is based.

from about 12g. at 70 mm. length to 35 g. at 105 mm. At about this point there is a discontinuity in the curve and above 110 mm. and 40 g. the increase in weight per unit of length was greater. Thus at lengths below 110 mm. an increase in body length by 10 mm. resulted in a mean increase of 7 g. in the mean body weight ; above 110 mm. a 10 mm. increase in length was associated with an increase in weight of about 10 g. At this stage males tended to become heavier than females of the same body length.

The length of the tail relative to the body length also varied (Fig. 3). At body lengths of 110 mm. and more, tail length increased regularly at all seasons but the rate of growth was less than that of the body so that the tail was relatively shorter in larger rats than in smaller ones and was shorter than the body. Body and tail lengths were approximately equal in rats with body lengths of 100 mm. but in smaller animals the relative lengths varied at different

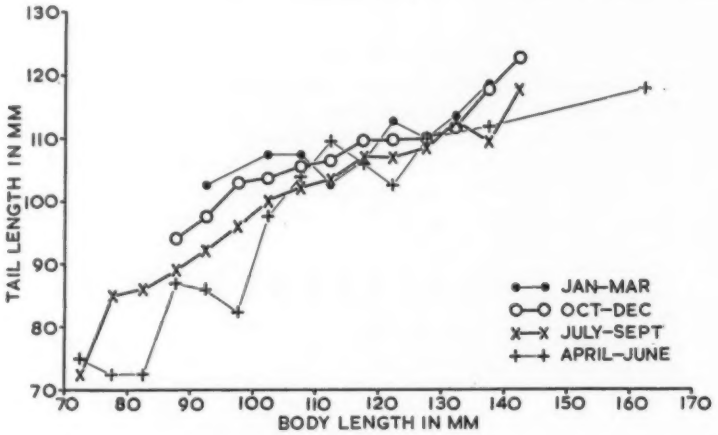

Fig. 3.—Tail length relative to body length of male rats, showing the different proportions in immature rats at different times of year.

times of year. Thus in all small rats from April to June body and tail lengths were approximately equal but from July to September tail length tended to exceed body length. This tendency became more marked, reaching a maximum in the few small rats remaining in the period from January to March. As an example male rats of body length 90 to 95 mm. may be considered. From April to June their mean tail length was 86 mm. ; this increased to 92 mm. from July to September, 97 mm. from October to December and finally to 102 mm. during the period January to March. These differences are statistically significant.

The reasons for these differences in the growth of the tail relative to the body are not known. They may be related to general differences in growth rate associated with adverse conditions, of high temperature and lack of food, at the end of the dry season in October and November. It is probable that

the rats which were still small during the period from January to March were born at this time. Growth relative to age may also be important and it is of interest that in large, mature rats the relative growth rates were similar for all seasons and sizes.

The discontinuity in the curve of tail length relative to body length is presumably associated with maturation. The break occurs at a body length of about 110 mm. in males and 105 mm. in females. Pirlot (1957) in the Belgian Congo also noted this variation in tail length according to size but did not record the seasonal differences.

A similar phenomenon was recorded in males in the length of the testes relative to body length (Fig. 4). A marked discontinuity is apparent in the

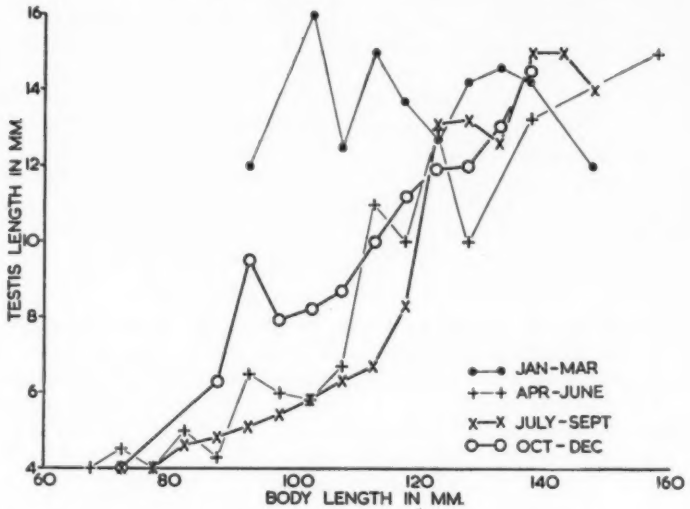

Fig. 4.—Testis length relative to body length in males, showing the different proportions in immature rats at different times of year.

curves between 110 mm. and 120 mm. body length. This is again presumed to be related to maturation and Pirlot (1957), using weights instead of lengths, observed a similar break. At body lengths greater than 115 mm. the testis was large and similar in length at all seasons but in smaller rats the size of the testis varied with the season as well as with the size of the rat. Thus in rats 105 mm. long the mean length of the testis from April to September was about 6·5 mm. This increased to 8·7 mm. in the period October to December and still further, to 12·5 mm., from January to March.

From January to March all the rats had large testes and were, presumably, mature. Large numbers of young were born from May onwards and it is probable that the upper parts of the curves for April to September (Fig. 4) represent the adult generation and the lower parts the new generation with testis length increasing linearly with body length. It is suggested that

the inflexion between the two parts of the curves represents the separation of the parent from the filial generation. Alternatively, this could represent the onset of puberty with rapid growth of the testes from the juvenile to the adult condition. However, the curve for October to December is almost linear, with very little trace of inflexion, which suggests that the change from the immature to the mature state is not a sudden phenomenon but takes place in a continuous and regular manner. If this is so the seasonal differences in testis size relative to body length are probably related to age.

The large size of the testes in all big rats indicates that there was no seasonal regression in the size of the gonads or, probably, of sexual activity. Rogers Brambell & Davis (1941) obtained no evidence that the males, once fecund, ever became non-fecund.

No comparable data are available for females but the few pregnant females which were obtained were more than 110 mm. long. Thus all the available data indicate that the rats became mature when they were about this size. The mean weight of male rats between 110 and 115 mm. long was 44 g. and that of females 40 g. These figures correspond well with those of Rogers Brambell & Davis (1941) who regarded male rats of 45 g. and over and females of 40 g. and over as being mature. Pirlot (1957) gave 40 g. as the weight above which all male rats could be regarded as mature, females maturing at a lower weight, and Oliff (1953) found that in the laboratory females matured at about 39 g. In the following section males of 45 g. and over and females of 40 g. and over are regarded as being mature.

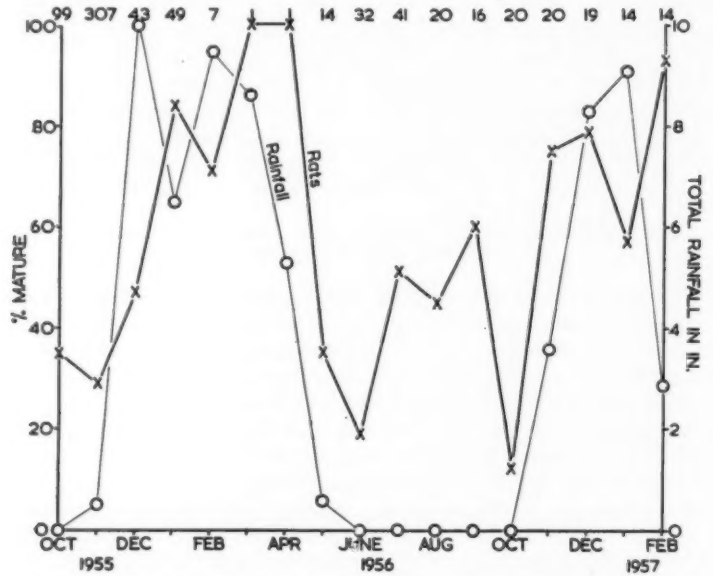

Fig. 5.—The percentage of mature rats obtained each month and the total monthly rainfall. Most rats were mature soon after the end of the rainy season.

BREEDING

The breeding season was determined from the percentages of mature rats which were obtained at different times of year (Fig. 5). The majority of rats were mature from January to April, 1956 and from November, 1956 until the end of the observations in February, 1957. Immature rats were common from October to December, 1955 and from May to October, 1956. If a given length is used as the criterion of maturity instead of weight it is apparent that immature rats were common from May to December, 1955, thus corresponding with the 1956 figures.

According to Johnston & Oliff (1954), pregnancy lasts for rather less than one month so that breeding must normally begin in April to produce the first young in May. Johnston & Oliff found maturation to occupy about three-and-a-half months and Fig. 5 shows that the percentage of immature rats started to fall off in November and December, suggesting that breeding was reduced after July or August. The few immature rats remaining in February were probably born in November and conceived in October. It appears that very little breeding can have occurred between October and April.

Very few pregnant females were caught, suggesting a difference in their behaviour compared with males and immature rats, but they were obtained from February to November, with rather more in April and May than in other months. Thus breeding occurred mainly at the end of the rainy season and the beginning of the dry season, which normally lasted from May to October. Rogers Brambell & Davis (1941) observed a similar peak of breeding at this time in Sierra Leone, although a few pregnant females were obtained at all times of year. Similarly Pirlot (1954) in the Belgian Congo records copulation and gestation in the latter part of the rainy season and continuing through the dry season.

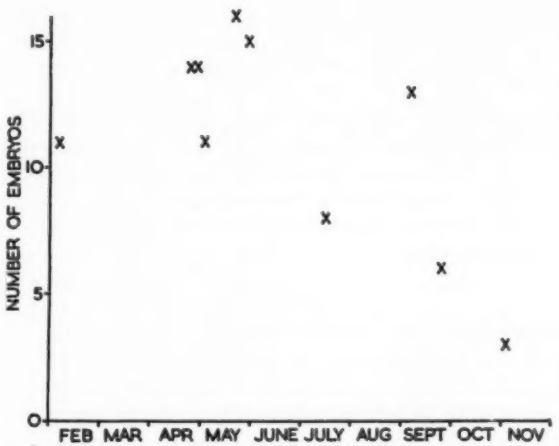

Fig. 6.—The number of embryos found in pregnant females at different times of year.

Breeding thus seemed to be at its peak when external conditions were most favourable. At this time of year the soil was still wet, but not waterlogged, and this was probably important in burrowing and nest building. Ground temperatures never became excessive during this period and there was ample vegetation for cover and for food.

NUMBER OF EMBRYOS

In ten pregnant females the number of embryos varied from three to sixteen with a mean of 11·2. There was some suggestion that the number of embryos present was less towards the end of the breeding season than it was earlier on (Fig. 6). This could have resulted from the generally adverse conditions, of high temperature, extreme dryness and lack of food, prevailing at this time. Rogers Brambell & Davis (1941) recorded seven to seventeen embryos, with a mean of 11·8, in Sierra Leone and in the laboratory Oliff (1953) obtained a mean litter size of 7·2, considering a population as a whole. The number of embryos was not related to the body weight of the mother.

DISCUSSION

Oliff (1953) calculated that a population of *R. natalensis* could multiply 1·5 times in 28 days. This, however, was considering the population as a whole with each female spending more than half its life in anoestrous and, as Johnson & Oliff (1954) point out, most propagation occurs when few females are in anoestrous. Rogers Brambell & Davis (1941) found some females in anoestrous at all times except at the height of the breeding season so that it seems likely that breeding throughout the population is co-ordinated, by an internal or external mechanism, and that during the peak of the breeding season the potential increase is of the order of five times per month. If there is a seasonal variation in litter size this figure might be even greater and this could be maintained for several months since oestrous follows soon after the birth of the young (Johnston & Oliff, 1954). In this way the tremendous increases in the rat populations at the beginning of the dry season can partly be accounted for.

Fig. 5 suggests that the rats born early in the year may breed at their first oestrous. The minimum in the curve in October, 1956 follows four months after that in June, this period corresponding with the time taken for the young to mature and breed. It is probably this breeding of the young rats in their first season which, added to the already high breeding potential of the parent generation, leads to plagues.

SUMMARY

The Multimammate Rat, *Rattus natalensis*, was present, often in very large numbers, near habitations in the Rukwa Valley, Tanganyika Territory. Weight, tail length and testis length in males relative to body length were different at body lengths above and beiow 110 mm., the difference being associated with maturation. The relative growth rates of different organs varied at different seasons.

Breeding occurred mainly at the end of the rainy season and the beginning of the dry season and the potential rate of increase of the adult population alone was of the order of five or more times per month over the peak of the breeding season. Plagues resulted from this and the additional breeding of young rats at their first oestrous.

ACKNOWLEDGMENTS

We are indebted to Mr D. H. S. Davis, Government Ecologist, Johannesburg, for confirming the identification of the rats and for his valuable advice. The data on numbers of rats caught in the grain stores were kindly supplied by Mr L. Van In and Mr A. J. Davis.

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THE MATERNAL AND NEONATAL WEIGHTS OF SOME MAMMALIA

BY

I. LEITCH

Commonwealth Bureau of Animal Nutrition, Bucksburn, Aberdeenshire

AND

F. E. HYTTEN AND W. Z. BILLEWICZ

Obstetric Medicine Research Unit (M.R.C.), Foresterhill, Aberdeen

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ORIGIN OF THE ENQUIRY

The stimulus to make this study was the statement of Dr R. M. Laws (1956) that " whales and seals, being aquatic animals are able to bear young which are larger, both absolutely and relatively, than the young of the larger terrestrial mammals." Dr Laws went on to say that the ratio of the weight of the newborn young to that of the mother is 1 : 30 (3·3 per cent.) for the elephant seal and 1 : 17 (5·9 per cent.) for the fin whale. The elephant seal is the largest of the seals and the breeding female weighs 1000 kg.; the fin whale is not the largest whale, but it weighs 50,000 kg.

From our common knowledge of the weights of human mother and infant, and of the mothers and young of the large domestic mammals such as the cow and buffalo, the ratios quoted for aquatic mammals were certainly not high, and we decided to investigate the relation more closely.

Dr Laws's idea of the relatively low weight of the young of the large land mammals derived from a table in Professor D'Arcy Thompson's book " On Growth and Form " (1942) which is reproduced here (Table 1).

TABLE I

The "Relative Weights of the New-born Animal and its Mother"
(From D'Arcy Thompson, 1942)

Bear	1 : 600	Sheep	1 : 14
Lion	160	Ox	13
Hippopotamus	45	Horse	12
Dog	45–50	Rabbit	40
Cat	25	Mouse	10–25
Man	22	Guinea-pig	7

In his table D'Arcy Thompson made no distinction between single births and the single young of multiple births or litters. The table is preceded by this statement: "It would seem to be a natural rule, that those offspring which are most highly organised at birth are those which are born largest relatively to their parents' size. But another rule comes in, which is perhaps less to be expected, that the offspring are born smaller the larger the species to which they belong". It is followed by this:

"These differences are for the most part made up quickly; in other words, there are great differences in the rate of growth during early post-natal life".

It was the growth process with which D'Arcy Thompson was concerned and the single young was from his point of view the relevant unit. But since the implication of Dr Laws's statement is that the anti-gravitational effect of water is to permit the mother to carry a heavier load of young, a comparison of ratios of which some refer to the whole load and others to a small part of it, is without meaning. The seal and the whale bear single young, but the lion has a litter of five and the pig of up to twenty.

THE DATA FOUND

Records of the weight of both mother and young are extremely difficult to find. It is easy to understand scarcity or absence of data for the large beasts of prey, but difficult to understand why small mammals are not more often weighed. We have read countless papers in which the habits and reproductive behaviour of small mammals are described in the greatest detail and linear measurements of the body are reported to fractions of a millimetre. Indeed about a very large number of mammals everything seems to have been recorded except weight. Nevertheless we have found some weights for animals in each of the orders of living mammals and of 114 species.

The ideal data from which to seek a biological law would be large numbers of paired weights of healthy, well-grown young adult females and their subsequent newborn offspring, but records of that sort have not been published for any mammal. The best that can be expected is weights of such young adults and of healthy newborn young. Even those exist, in record form, only for man and laboratory mammals. For farm animals the knowledge is more often traditional than statistical; even in experimental flocks of ewes, weight at lambing is usually recorded, not weight at mating. We have therefore chosen where possible to present in the main table and to illustrate subsidiary arguments with data from experiments, even with small numbers of animals,

in which the animals can be confidently taken to be normal representatives of their breed and strain and the data are accurately recorded paired measurements taken at, or so near as not to matter to, mating and birth.

For some species, such as the hippopotamus, only chance records of weights of individual mothers and offspring have been found and these may not be typical of the species. It is not possible to judge.

Most of our data fall between the two extremes of accurate experimental and purely chance observations, and refer to average weights of a few adult females and a few, often unrelated, newborn young. That being so, we had no high expectation of finding any close and easily demonstrated relation between the two. In that we were mistaken.

RESULT OF ANALYSIS

The results are presented in Table 2 and two figures. In Fig. 1 the logarithm of the weight of the young is plotted against the logarithm of the weight of the mother. The relation is obviously a straight line on which lie both the tiny 6 and 7 gram bats and the Blue whale with a weight at maturity of more than 10 million times that of the bats.

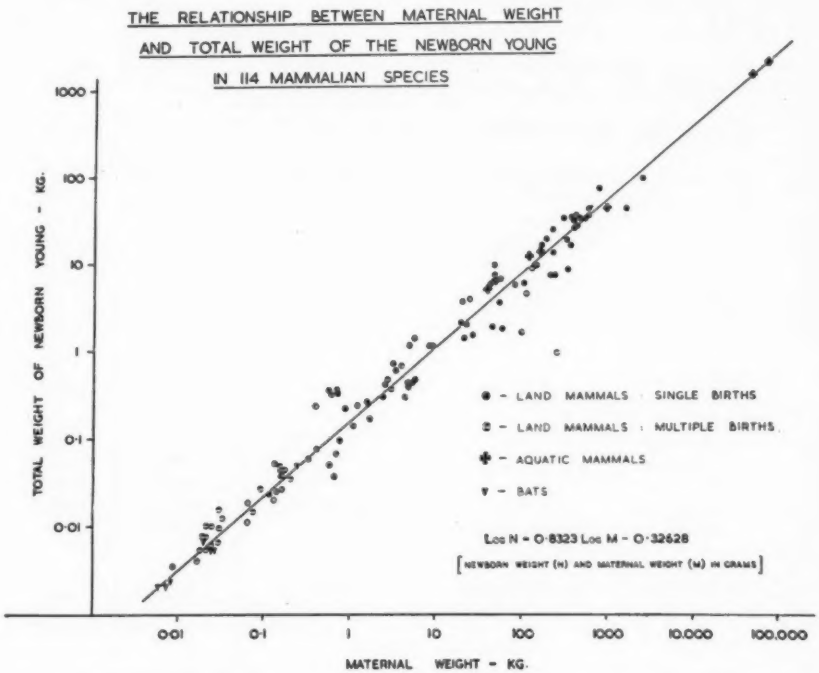

Fig. 1.—The logarithm of the weight of the young plotted against the logarithm of the weight of the mother.

TABLE

Species	Weight of mother	Weight of single young	Number of young*
Man (*Homo sapiens*)	56 kg.	3·2 kg.	1
Gorilla (*Gorilla gorilla*)	60 kg.	1·75 kg.	1
Chimpanzee (*Pan* sp.)	46·2 kg.	1·8 kg.	1
Macaque (*Macacus rhesus*)	5290 g.	430 g.	1
Java macaque (*Macaca irus mordax* Thomas and Wroughton)	2450 g.	310 g.	1
Wanderoo (*Macaca* sp.)	5000 g.	380 g.	1
Marmoset (*Hapale jacchus* L.)	335 g.	30 g.	2
Tarsier (*Tarsius spectrum*)	114 g.	23·5 g.	1
Fruit bat (*Eidolon helvum*)	250 g.	50 g.	1
Greater horseshoe bat (*Rhinolophus ferrumequinum*)	19·7 g.	6·8 g.	1
Lesser horseshoe bat (*Rhinolophus hipposideros*)	6·1 g.	2·1 g.	1
Long-eared bat (*Plecotus auritus*)	8·3 g.	2·45 g.	1
Noctule bat (*Nyctalus noctula*)	27·5 g.	5·65 g.	1
Serotine bat (*Eptesicus serotinus*)	25 g.	4·8 g.	1
Little brown bat (*Myotis lucifugus lucifugus*)	7·2 g.	2·08 g.	1
Hedgehog (*Erinaceus europaeus*)	725 g.	13·9 g.	7
Hedgehog (*Erinaceus roumanicus*)	700 g.	18 g.	2
Shrew (*Blarina brevicauda* Say)	16·6 g.	0·8 g.	5
Duplicidentata			
Wild rabbit (*Oryctolagus cuniculus*)	1175 g.	42·5 g.	5·24
Rabbits, domestic :			
Himalayan	1700 g.	40 g.	4
Old English × Chinchilla	3200 g.	81 g.	9
Himalayan $\frac{H}{C}$	2625 g.	80 g.	5
Snowshoe hare (*Lepus americanus phaeonotus* Allen)	1598 g.	85 g.	3
Cretan hare (*Lepus europaeus creticus*)	3000 g.	123 g.	3
Simplicidentata			
Grey squirrel (*Sciurus carolinensis*)	600 g.	15 g.	3·2
Thirteen-striped ground squirrel (*Citellus tridecemlineatus* Mitchell)	160 g.	2·6 g.	10

* The number of young stated is the number known or believed to be typical, or, where decimal points occur, the average number at two or more births for which the corresponding mean weights are given.

Total weight of litter	Litter weight / Maternal weight × 100	Reference
PRIMATES		
3·2 kg.	5·7	Aberdeen Maternity Hospital.
1·75 kg.	3·0	Brandes, C., 1930. *Zool. Gart., Leipzig* **3,** 104 (young). Census of Gorillas outside Africa, 1953–55. *Zool. Gart., Leipzig* **20,** 176 (adult). Grzimek, B., 1956. *Z. Säugetierk.* **21,** 192.
1·8 kg.	3·9	Elder, J. H. & Yerkes, R. M., 1936. *Proc. Roy. Soc.* (B) **120,** 409. Savan, J. A., 1952. *Amer. J. Phys. Anthropol.* **10,** 23.
430 g.	8·1	Hartman, C., 1928. *J. Mammal.* **9,** 181 ; *Zool. Gart., Leipzig* 1929, **1,** 342.
310 g.	12·9	Spiegel, A., 1930. *Arch. Gynäkol.* **142,** 561.
380 g.	7·6	*Zool. Gart., Leipzig,* 1939–40, **11,** 119.
60 g.	17·9	Lucas, N. S., Hume, E. M. & Smith, H. H., 1937. *Proc. zool. Soc. Lond.* (A) **107** 205.
23·5 g.	20·6	Le Gros Clark, W. E., 1924. *Proc. zool. Soc. Lond.* **1924,** 217.
CHIROPTERA		
50 g.	20·0	Eisentraut, M. (Personal communication).
6·8 g.	34·5	Hooper, J. H. D. & Hooper, W. M., 1956. *Proc. zool. Soc. Lond.* **127,** 1.
2·1 g.	34·4	Hooper, J. H. D. & Hooper, W. M., 1956. *Proc. zool. Soc. Lond.* **127,** 1.
2·45 g.	29·5	Eisentraut, M. (Personal communication).
5·65 g.	20·5	Eisentraut, M. (Personal communication).
4·8 g.	19·2	Eisentraut, M. (Personal communication).
2·08 g.	28·9	Smith, E., 1956. *Amer. J. Physiol.* **185,** 61.
INSECTIVORA		
98 g.	13·5	Herter, K., 1933. *Z. Säugetierk.* **8,** 195.
36 g.	5·1	Stein, G., 1929–30. *Z. Säugetierk.* **4,** 240.
4·0 g.	24·1	Pearson, O. P., 1944. *Amer. J. Anat.* **75,** 39.
RODENTIA		
233 g.	18·6	Brambell, F. W. R., 1944. *Proc. zool. Soc. Lond.* **114,** 1.
160 g.	9·4	Catalogue of Uniform Strains of Laboratory Animals maintained in Great Britain. Laboratory Animals Bureau, London, 1953.
729 g.	22·8	
400 g.	15·4	
255 g.	15·9	Grange, W. B., 1932. *J. Mammal.* **13,** 1.
370 g.	12·6	Zimmerman, K., 1953. *Z. Säugetierk.* **17,** (1942–49), 21.
48·5 g.	8·1	Shorten, M., 1951. *Proc. zool. Soc. Lond.* **121,** 427.
26 g.	16·3	Wade, O., 1927. *J. Mammal.* **8,** 269.

TAB[illegible] [Con

Species	Weight of mother	Weight of single young	Number of young*	Tota of
Simplicidentata [Contd.]				
Kangaroo rat (*Dipodomys spectabilis baileyi* Goldman)	135 g.	7·7 g.	2·6	2
Beaver (*Castor* sp.)	24·3 kg.	0·34 kg.	6	
Harvest mouse (*Reithrodontomys montanus albescens* Cary)	8·5 g.	1·2 g.	2·9	
Prairie deermouse (*Peromyscus maniculatus*)	21·3 g.	1·8 g.	4	
Desert woodrat (*Neotoma lepida lepida*)	140 g.	10·4 g.	2·3	2
Dwarf hamster (*Cricetulus barabensis griseus*)	30 g.	1·8 g.	5·3	
Red-backed vole (*Clethrionomys glareolus*)	20 g.	1·9 g.	4	
Muskrat (*Ondatra zibethica*)	1103 g.	21·3 g.	6·5	13
Northern pine mouse (*Pitymys pinetorum scalopsoides*)	27·5 g.	2·2 g.	3	
Vole (*Microtus californicus*)	63 g.	2·7 g.	5	1
(*Microtus oeconomus stimmingi* Nehring)	30 g.	2·6 g.	5	1
(*Microtus arvalis*)	31 g.	1·85 g.	8·5	1
Gerbil (*Tatera brantsi*)	75 g.	5·5 g.	2·6	1
(*Tatera afra*)	65 g.	4·5 g.	4	1
Black rat (*Rattus rattus* L.)	90 g.	4·5 g.	5·6	2
Laboratory rats :				
Wistar albino	160 g.	5·7 g.	6·5	3
PVG/C hooded	138 g.	8·6 g.	6	5
WAG/C albino	145 g.	6 g.	8	4
Wistar albino	170 g.	5·5 g.	8	4
Lister hooded	205 g.	5 g.	7	3
WAG	160 g.	5 g.	8·7	4
House mouse (*Mus musculus*)	25 g.	1·25 g.	8	1
Laboratory mice :				
Swiss albino	25 g.	1·02 g.	6	
Swiss albino	22 g.	2·0 g.	5	1
Webster's Rockefeller	20 g.	1·0 g.	5	
Vermont jumping mouse (*Napaeozapus* sp.)	22 g.	1 g.	5	
New World porcupine (*Erithizon dorsatum*)	6000 g.	482 g.	1	48
Guinea-pig (*Cavia porcellus*), laboratory :				
Black, brown and white	400 g.	78·5 g.	3	23
Frant albino	560 g.	95 g.	3·7	35
Abyssinian	700 g.	80 g.	4	32
Albino	600 g.	90 g.	3·5	31
Albino	700 g.	93·4 g.	3·6	33

[Continued]

Total weight of litter	Litter weight / Maternal weight × 100	Reference
20 g.	14·8	Holdenreid, R., 1957. *J. Mammal.* **38**, 330.
2·0 kg.	8·2	Shadle, A. R., 1930. *J. Mammal.* **11**, 483.
	" 2 weeks from term "	
3·4 g.	40·0	Leraas, H. J., 1938. *J. Mammal.* **19**, 441.
7·2 g.	33·8	Svihla, A., 1934. *J. Mammal.* **15**, 99 ; Svihla, A., 1935. *J. Mammal.* **16**, 109.
23·8 g.	17·0	Egoscue, H. J., 1957. *J. Mammal.* **38**, 472.
9·5 g.	31·7	Herter, K. & Rauch, H. G., 1956. *Z. Säugetierk.* **21**, 161.
7·6 g.	38·0	Wrangel, H. v., 1940. *Z. Säugetierk.* **14**, 52.
138·5 g.	12·6	Errington, P. L., 1939. *J. Mammal.* **20**, 465.
6·6 g.	24·0	Hamilton, W. H., 1938. *J. Mammal.* **19**, 163.
11·2 g.	17·8	Selle, R. S., 1928. *J. Mammal.* **9**, 93.
13·0 g.	43·3	Frank, F. & Zimmermann, K., 1956. *Z. Säugetierk.* **21**, 58.
15·6 g.	50·3	Frank, F., 1956. *Z. Säugetierk.* **21**, 176.
14·5 g.	19·3	Measroch, V., 1954–55. *Proc. zool. Soc. Lond.* **124**, 631.
18 g.	27·5	
25·2 g.	28·0	Kelway, P. & Thompson, H. V., 1957. The UFAW Handbook on the Care and Management of Laboratory Animals. 2nd Ed., p. 378. UFAW, London.
37 g.	23·2	Catalogue of Uniform Strains of Laboratory Animals Maintained in Great Britain. Laboratory Animals Bureau, London, 1953.
52 g.	37·7	
48 g.	33·1	
44 g.	25·9	
35 g.	17·1	
43·5 g.	27·2	
10 g.	40·0	Tuffery, A. A., 1957. The UFAW Handbook on the Care and Management of Laboratory Animals. 2nd Ed., p. 243, UFAW, London.
6·1 g.	24·4	Catalogue of Uniform Strains of Laboratory Animals maintained in Great Britain. Laboratory Animals Bureau, London, 1953.
10 g.	45·5	
5 g.	25·0	
5 g.	22·7	Sheldon, C., 1938. *J. Mammal.* **19**, 444.
482 g.	8·0	Wynne-Edwards, V. C. (Personal communication) ; Struthers, P. H., 1928. *J. Mammal.* **9**, 300 ; Shadle, A. R. & Ploss, W. R., 1943. *J. Mammal.* **24**, 492.
236 g.	59·0	Catalogue of Uniform Strains of Laboratory Animals maintained in Great Britain. Laboratory Animals Bureau, London, 1953.
352 g.	63·0	
320 g.	45·7	
315 g.	52·5	
336 g.	48·0	Paterson, J. S., 1957. The UFAW Handbook on the Care and Management of Laboratory Animals. 2nd Ed., p. 203. UFAW, London.

TABLE

Species	Weight of mother	Weight of single young	Number of young*
Capybara (*Hydrochoerus isthmius* Goldman)	20·5 kg.	1·2 kg.	3
Mountain viscacha (*Lagidium* sp.)	908 g.	227 g.	1
Nutria (*Myocastor* sp.)	3500 g.	201 g.	3·1
	5100 g.	251 g.	4·6
	5410 g.	235 g.	6
Giant ant-eater (*Myrmecophaga* sp.)	28 kg.	1·48 kg.	1
Six-banded armadillo (*Euphractus* sp.)	4635 g.	144 g.	2
Blue whale (*Sibbaldus* sp.)	79,000 kg.	2000 kg.	1
Fin whale (*Balaenoptera* sp.)	50,000 kg.	1500 kg.	1
Porpoise (*Phocaena phocaena* L.)	50 kg.	6·5 kg.	1
Pinnipedia			
Elephant seal (*Mirounga leonina* L.)	1000 kg.	45 kg.	1
Grey seal (*Halichoerus grypus*)	169 kg.	13·6 kg.	1
Harp seal (*Phoca groenlandica*)	120 kg.	11·8 kg.	1
Fur seal (*Callorhinus ursinus*)	40·5 kg.	5·1 kg.	1
Arctoidea			
Sea otter (*Enhydra lutris* L.)	20 kg.	2·0 kg.	1
Sea otter (*Enhydra lutris nereis*)	21·8 kg.	1·36 kg.	1
Spotted skunk (*Mephitis* sp.)	500 g.	10 g.	7
Ferret (*Putorius furo* L.)	700 g.	9 g.	7·5
Black bear (*Ursus americanus*)	100 kg.	0·31 kg.	5
Polar bear (*Ursus maritimus*)	258 kg.	0·59 kg.	1·5
Cynoidea			
Silver fox (*Vulpes* sp.)	5000 g.	110 g.	3·8
Red fox (*Vulpes fulva*)	4200 g.	100 g.	6·8
Dog : " terrier "	9870 g.	203 g.	5·3
Cocker spaniel	8400 g.	228 g.	4·9
Aeluroidea			
Lion (*Felis leo*)	114 kg.	0·89 kg.	5
Cat, domestic	2750 g.	113 g.	4

[Continued]

Total weight of litter	Litter weight / Maternal weight × 100	Reference
3·6 kg.	17·6	Trapido, H., 1949. *J. Mammal.* **30,** 433.
227 g.	25·0	Pearson, O. P., 1949. *Amer. J. Anat.* **84,** 143.
623 g.	17·8	Oleinikov, N. S., 1954. *Karakul. Zver.* **7,** No. 6, 45.
1155 g.	23·5	
1410 g.	25·9	Olsson, N., 1956. *Deutsch. Pelztierz.* **30,** 21.
EDENTATA		
1·48 kg.	5·4	Honigmann, H., 1935. *Z. Säugetierk.* **10,** 78.
288 g.	6·2	*Zool. Gart., Leipzig* 1953–55, **20,** 83.
CETACEA		
2000 kg.	2·5	Krogh, A., 1934. *Nature* **133,** 635.
1500 kg.	3·0	Laurie, A. M. 1933. '*Discovery Rep.*' **7,** 363; Mackintosh, N. A., 1942. '*Discovery*' *Rep.* **22,** 197.
6·5 kg.	13·0	Slijper, E. J., 1956. *Hvalrådets Skr.* No. 41, Oslo.
CARNIVORA		
45 kg.	4·5	Laws, R. M., 1953. *Sci. Rep.* No. 8. *Falkland Is. Dept. Survey.*
13·6 kg.	8·0	Amoroso, E. C. & Mathews, J. H., 1951. *J. Anat.* **85,** 427.
11·8 kg.	9·8	Sivertsen, E., 1941. *Hvalrådets Skr.* No. 26, Oslo.
5·1 kg.	12·6	Scheffer, V. B. & Wilke, F., 1953. *Growth* **17,** 129.
2·0 kg.	10·0	Barabash-Nikiforov, I., 1935. *J. Mammal.* **16,** 255. (Maternal weight adjusted).
1·36 kg.	6·3	Quoted from Pearson, O. P., 1952. *J. Mammal.* **33,** 387.
70 g.	14·0	Crabb, M. D., 1944. *J. Mammal.* **25,** 213.
68 g.	9·7	Murr, E., 1935. *Z. Züchtung* (B) **32,** 269, 385.
1·6 kg.	1·6	Hamilton, W. J., 1939. American Mammals, N.Y. and Lond., p. 189; Seton, E. T., 1909. Life Histories of Northern Animals. N.Y., p. 1052–3.
0·89 kg.	0·3	Schneider, K. M., 1933. *Zool. Gart., Leipzig* **6,** 156.
418 g.	8·4	Firstov, A. A. & Haritonov, P. A., 1957. *Karakul. Zver.* **1957,** No. 2, 27.
680 g.	16·2	Hoffman, R. A. & Kirkpatrick, C. M., 1954. *J. Mammal.* **35,** 504; Sheldon, W. G., 1949. *J. Mammal.*, **30,** 236.
1083 g.	11·1	Lössl, H., 1932. *Z. Hündeforsch.* **2,** No. 3–4.
1118 g.	13·0	Siedler, A. J. & Schweigert, B. S., 1954. *J. Nutrition* **53,** 187. (Basal group only).
4·4 kg.	3·9	Mathews, L. H., 1957. (Personal communication).
452 g.	16·1	Dickinson, C. D. & Scott, P. P., 1956. *Brit. J. Nutrition* **10,** 311.

TABLE

Species	Weight of mother	Weight of single young	Number of young*
Elephant (*Elephas* sp.)	2590 kg.	93 kg.	1
Horse (*Equus caballus* L.)			
Shire	800 kg.	71·0 kg.	1
Shetland pony	191 kg.	19·6 kg.	1
Tapir (*Tapirus* sp.)	250 kg.	7 kg.	1
Pig (*Sus* sp.) :			
Hannover-Braunschweig	163 kg.	1·14 kg.	8·36
Landschwein	130 kg.	1·16 kg.	7·94
Duroc Jersey, 1st mating	79 kg.	—	—
Dwarf hippopotamus (*Choeropsis* sp.)	225 kg.	6·75 kg.	1
Hippopotamus (*Hippopotamus* sp.)	1750 kg.	40 kg.	1
Elk (*Alce* sp.)	377 kg.	16 kg.	1
Reindeer (*Rangifer* sp.)	105 kg.	5·6 kg.	1
Buffalo (*Bubalus* sp.):			
Indian	550 kg.	34 kg.	1
Indian, first mating	319 kg.	36 kg.	1
Italian	595 kg.	37·2 kg.	1
Russian	419 kg.	30·7 kg.	1
Phillipine carabao	484 kg.	32 kg.	1
Yak (*Bos* sp.)	233 kg.	13·2 kg.	1
Pamirs	356 kg.	8·4 kg.	1
Cattle (*Bos* sp.) :			
Holstein	600 kg.	40·8 kg.	1
Jersey	430 kg.	25·4 kg.	1
Sindhi	336 kg.	18·6 kg.	1
Bǎua	175 kg.	15·8 kg.	1
Dølafe	385 kg.	31 kg.	1
Sid. Trønder	313 kg.	32 kg.	1
Raukolle	405 kg.	31·7 kg.	1
Telemark	408 kg.	26 kg.	1
NRF	400 kg.	34 kg.	1
Goat (*Capra* sp.) :			
Jugoslav × Saanen	45 kg.	3·5 kg.	1
		2·93 kg.	2
		1·9 kg.	3
British Saanen	62 kg.	3·2 kg.	2
Sheep (*Ovis* sp.) :			
Border Leicester	50 kg.	4·9 kg.	1
	52·3 kg.	3·65 kg.	2
Welsh	26·8 kg.	2·9 kg.	1
	26·8 kg.	1·95 kg.	2
Wiltshire	80 kg.	4·95 kg.	2
	80 kg.	3·7 kg.	3

[Continued]

Total weight of litter	Litter weight / Maternal weight × 100	Reference
PROBOSCIDEA		
93 kg.	3·6	*Zool. Gart., Frankfurt*, 1887, **28**, 337 ; *Zool. Gart., Frankfurt*, 1865, **6**, 233 ; *Zool. Gart., Leipzig*, 1933, **6**, 144, 197 ; *Zool. Gart., Leipzig*, 1932, **5**, 170 ; *Zool. Gart., Leipzig*, 1951, **18**, 14 ; FLOWER, S. S., 1943. *Proc. zool. Soc. Lond.* **113**, 21.
PERISSODACTYLA		
71 kg.	8·9	WALTON, A. & HAMMOND, J., 1938. *Proc. Roy. Soc.* (B) **125**, 311.
19·6 kg.	10·3	
7 kg.	2·8	SCHNEIDER, K. M., 1936. *Zool. Gart., Leipzig*, **8**, 83 ; *Z. Säugetierk.* 1938–39, **13**, 57.
ARTIODACTYLA		
9·5 kg.	5·8	DSCHAPARIDSE, D., 1935. *J. Landwirtsch.* **83**, 161.
9·2 kg.	7·1	
5·4 kg.	6·8	GRISWOLD, J. D. *et al.*, 1928. *Missouri Res. Bull.* No. 114.
6·75 kg.	3·0	STEINMETZ, H., 1937. *Zool. Gart., Leipzig* **9**, 255.
40 kg.	2·3	
16 kg.	4·2	KNORRE, E. P. & KNORRE, E. K., 1956. *Zool. Z.* **35**, 1229.
5·6 kg.	5·3	MERTZ, P. A., 1939. *Trud. Biol. Inst. Tomsk. Univ.* **6**, 175.
34 kg.	6·2	HAFEZ, E. S. E., 1954. *J. Agric. Sci.* **46**, 137.
36 kg.	11·3	
37·2 kg.	6·3	MAYMONE, B., 1942. *Z. Tierz. Züchtungsbiol.* **52**, 1.
30·7 kg.	7·3	KALUGIN, I. I., 1936. *Trud. Vet. Zooteh. Inst. Erevan* **1**, 179.
32 kg.	6·6	VILLEGAS, V., 1939. *Phillipine Agric.* **28**, 253.
13·2 kg.	5·7	KOŽARIN, F. S., 1933. *Skotovodstvo*, 1933, No. 11/12, 40.
8·4 kg.	2·4	SINICYN, B. I., 1935. *Probl. Životn.* **8**, 113.
40·8 kg.	6·8	BRODY, S., 1945. Bioenergetics and Growth, p. 460.
25·4 kg.	5·9	
18·6 kg.	5·5	DOVE, C. N., 1941. *Poona Agric. Coll. Mag.* **33**, 24.
15·8 kg.	9·0	RAKO, A., 1943. *Vet. Arh.* **13**, **89.**
31 kg.	8·1	HVIDSTEN, H. (Personal communication).
32 kg.	10·2	
31·7 kg.	7·8	
26 kg.	6·4	
34 kg.	7·7	
3·5 kg.	7·8	RAKO, A., 1950. *Schweiz. Arch. Tierheilk.* **92**, 305.
5·9 kg.	13·1	
5·8 kg.	12·9	
6·4 kg.	10·3	CHALMERS, M. I. (Personal communication).
4·9 kg.	9·8	DONALD, H. P. (Personal communication).
7·3 kg.	14·0	
2·9 kg.	10·8	
3·9 kg.	14·6	
9·9 kg.	12·4	
11·1 kg.	13·9	

Mr W. Z. Billewicz has examined the data statistically and made the following comments.

A regression was fitted by the method of least squares, omitting laboratory rats and mice and guinea-pigs for reasons to be discussed below. For sheep the weight of twins was taken as normal for the mature ewe. The equation to the line is :

$$\log N = 0{\cdot}8323 \log M - 0{\cdot}32628$$

where N is the weight of the newborn young and M is the weight of the mother, both in grams.

Next, separate regressions were fitted to the data for single and multiple births. The difference between the lines was too small to justify separate treatment and the equation may be taken as best fit for both sets.

To predict the weight of young carried from the weight of a mother, the following equation has been derived from that above :

$$N = 0{\cdot}5408\ M^{\,0{\cdot}8323}$$

where N is the weight of young and M the weight of mother as before.

There are large deviations from the regression line, of which some are true

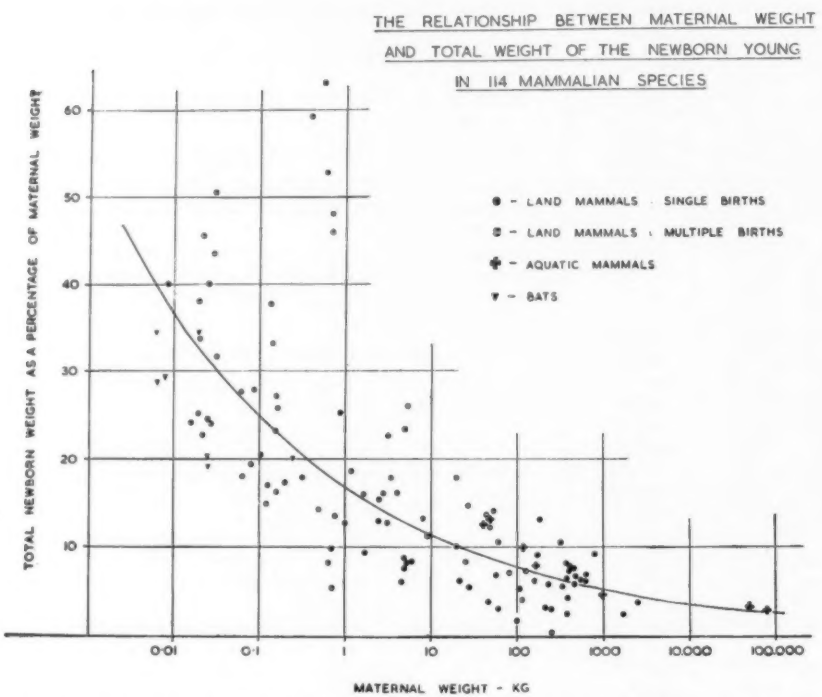

Fig. 2.—Showing that the weight of young is relatively greater the smaller the species to which they belong.

differences and not due to sampling errors ; for instance the weight of the bear's litter, which gives the most aberrant point on the negative side, and the guinea-pig's, which gives the biggest deviation on the positive side. When such true differences have been allowed for, there is still substantial variation, but not more than might be expected from a collection with so much haphazard data.

Fig. 2, in which the weight of young as a percentage of maternal weight is related to maternal weight, shows that the weight of young is relatively greater the smaller the species to which they belong. In respect of the weight of young carried, the aquatic mammal is not noticeably different from the terrestrial mammal of comparable size. But, at least in this collection, the seals are the only carnivores to bear single young so that, individually, they are large. The other carnivores have litters, up to seven in number.

DISCUSSION

Before we discuss causes of variation, a comment seems in place on the statements from D'Arcy Thompson, quoted above. The statement that the young " most highly organised at birth ", taking most highly organised to be synonymous with most mature, are relatively biggest, is true only within limits. It is not true in broad species comparisons. The newborn whale, which must surely be one of the most mature at birth, weighs only 3 or 4 per cent. of its mother's weight, and the horseshoe bat which has a percentage of 34, the highest of all, is born blind. That the offspring are born (relatively) smaller the larger the species to which they belong is true in general of total weight of young, whether the birth be multiple or single.

Sources of variation within a species

First of these is the difficulty, to which we have made reference already, of getting a sample at all, because zoologists rarely weigh. Huxley in 1927 who reanalysed Heinroth's (1922) data for birds commented on the reluctance of ornithologists to weigh, and the defect seems to be general among naturalists. Loveridge (1923) in notes on what must have been a large and highly organized expedition to East Africa to collect animals describes the weight of a female civet as " over 7 lb. (The scale only weighed to seven)." Since all the linear measurements are given in the metric scale it might be thought that the 7 lb. scale was not even official, but borrowed from the cook. Because of this reluctance to weigh, such data as exist are haphazard and subject to every known cause of variation.

Age at first breeding

When breeding is delayed much beyond the age at which an animal will mate under natural conditions, the performance deteriorates. The effect on the laboratory rat is shown in Table 3. It is perhaps unlikely to be of much significance in undomesticated animals.

Parity

Mothers that breed at sexual maturity and before they have finished growing have absolutely lighter young and fewer young in their first season than they

TABLE 3

The effect of maternal maturity at first breeding on the relative weight of the newborn litter

Species	Mothers			Newborn		
	Average age (days)	No.	Average weight (g.)	Average no. per litter	Average litter weight (g.)	Litter weight / Maternal weight × 100
Rat (Lister hooded)	90	10	240	12·0	70	28·5
	120	10	261	11·3	66	25·2
	200	15	324	9·1	52	16·1

will have in later pregnancies, though relatively the total weight may be greater. Number in a litter and weight of the individual young increase, usually to the third parity, remain at that level for a varying number of births, and then decline. Table 4 illustrates the change in ewes. The Scottish Blackface seldom or never has twins in its first season when it has attained little more than 80 per cent. of its mature weight, but the much smaller Welsh ewe which is almost fullgrown at eighteen months of age does have twins and shows no improvement of performance in its second season.

TABLE 4

Effect of weight and age of ewe on birth weight of lamb.

Breed	Ewes No.	Age years	Weight kg.	Weight of lamb	
				kg.	per cent. of ewe's weight
Scotti.h Blackface	9	1½	41·8	3·5	8·4 Single only
	8	2½	48·6	3·9	8·0 Single
	12		51·8	6·3	12·2 Twins
Welsh	166	1½	25·0	2·5	10·0 Single
	15			3·9	15·8 Twins
	165	2½	25·9	2·6	10·0 Single
	22			4·1	15·8 Twins
	149	3½	26·8	2·9	10·8 Single
	44			3·9	14·6 Twins

Weight of mother

In addition to the information in the main table, the following records (Table 5) were chosen to show that, within the species *Ovis*, the ratio of weight of lamb to weight of ewe appears to be almost independent of the size of the ewe, with the Welsh ewe as a possible exception.

TABLE 5

Effect of weight of ewe : different breeds

Breed	Weight of ewe	Mean weight of lamb		
	kg.	kg.	per cent. of ewe's weight	
German :				
Ewes 1½ years old when bred				
White-headed mutton	70	5·0	7·1	
Merino Landschaf	62·5	4·5	7·2	
Leineschaf	50	4·2	8·4	
Heidschnucken	30	2·2	7·4	
British :				
Ewes 2½ years old when bred				
Corriedale	68·1	5·2	7·6	Single
		7·8	11·5	Twins
Romney	65·4	4·6	7·0	Single
		7·6	11·6	Twins
Welsh	25·9	2·6	10·0	Single
		4·1	15·8	Twins

Nutrition

Both number and size of young are affected by the state of nutrition of the mother. She should be well fed but not overfed. In a chance assembly such as we have produced, there are almost certainly well and ill fed mothers to increase the variation. There might also be prematurely born young, but records known to be or suspected of being for premature young were rejected.

It seems likely that if records were available from mothers uniform in respect of these causes, the range of variation would be very much less. As it stands the prediction value of the line may not be high, but, in view of the spectacular range of maternal weights which it covers, it does appear to embody a natural law.

Differences between species

State of maturity at term

Differences in state of maturity at birth are very great. The whale, which is dropped into the water, must obviously be able to swim at once and to follow its mother. The seals, too, are abandoned soon after birth and must be born at an advanced stage of development. Among the large land mammals the foal, calf, lamb and goat are all almost able to fend for themselves at birth. At the opposite extreme the bear is no better, possible less, developed at birth than the young pig or most of the rodents.

The extreme example of immaturity is the marsupial. Lyne & Verhagen (1957) give several measurements of the young of *Trichosurus vulpecula* but no weight before about 100 days of age. Sharman (1957) gives the weight of the single young quokka (*Setonix brachyurus* Quoy and Gaimard, 1830)

" within a day of birth " as 0·45 gram, but that of the Native Cat (*Dasyurus viverrinus*) with a litter of from three to eighteen, more often four to six, averaged only 12·6 milligrams. The interesting thing in the present context is that the weight of the individual young " free in pouch " is about 100 grams and, if we assume a litter of five with a maternal weight of 2·2 kilograms, the ratio of litter weight to maternal weight is nearly 23 per cent., in good agreement with the weight at birth of other mammals with the same maternal weight.

Effect of selective breeding

The outstanding exception among rodents is the laboratory guinea-pig. Flower & Lydekker (1891) say that its ancestor is probably the South American Restless Cavy (*Cavia porcellus*) which produces one, or at most two, young at a birth. The laboratory guinea-pig may produce up to six young and most often produces three or four. Like those of other polytocous species, the young in large litters are individually smaller than those in small litters, but, in the guinea-pig, it is not the litter, but the *individual in a litter of three or four*, whose weight, as a percentage of maternal weight, fits our general relation. Hence the laboratory guineapig, as the result of selective breeding, is more prolific than its ancestor, and it looks as if it might also be absolutely larger at birth. The single guinea-pig at birth weighs up to 27·5 per cent. of its mother's weight and she is distinguished among mammals tested by her response to the special hormone, relaxin, which separates the pubic bones at the symphysis to facilitate birth.

Laboratory rats and mice and commercially farmed fur bearing animals also are selectively bred for size of litter, or size of young, or both and, in respect of litter weight, they deviate to the upper side, though much less than the guinea-pig. Laboratory rodents were omitted when the equation to the straight line in Fig. 1 was calculated.

Comparison with birds

In his monumental collection Heinroth (1922) had weights of birds of 432 species and of their eggs. He presented his data in tables and graphs showing weight of a single egg as a percentage of the weight of the hen bird, to show that, taking birds all together, or in separate groups, relative egg weight falls as absolute bodyweight increases, just as we have shown that relative weight of young does in mammals. With the very large numbers he had he was able to show also that the general curve is a composite of curves which differ in shape from one group to another. We have not enough data to judge whether subgroups exist among mammals.

Huxley, who reanalysed Heinroth's data in 1927, grouped the birds in ten groups whose weights fell within certain arbitrary limits and for each of these and the whole lot he related the logarithms of weight as we have done for mammals. In birds the relation is not a straight line. All the curves " tend to start steeper and to end flatter ".

Huxley's plea that " Accurate weight-measurements should be as much a matter of systematic routine as accurate length measurements or colour-descriptions " does not appear to have brought any great harvest yet, to

judge from our experience. Surely it is not too much to ask that field investigations should be equipped with simple apparatus to weigh. Spring balances are not really difficult to carry and if Dr R. M. Laws can set up tripods and spring balances to weigh 1000 kilogram seals, and even whales have been weighed piecemeal, there is no good or sufficient reason why we should not have records of weight as a routine.

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SUMMARY

When a comparison is made between maternal weight and weight of young in mammals the significant relation is of maternal weight to total weight of young at a birth.

A collection of data for 114 species is presented. The logarithms of maternal and newborn weights have a straight line relation from bats to whales. Relatively the larger mammals carry a smaller weight of young.

Sources of variation in the ratio of weight of young to weight of mother are discussed and a brief comparison is made with the results of Heinroth's analysis of weights of birds and their eggs.

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ON A FOURTH COLLECTION OF REPTILES, MOSTLY TAKEN IN TANGANYIKA TERRITORY BY MR C. J. P. IONIDES

BY
ARTHUR LOVERIDGE
Varneys, St. Helena Island, South Atlantic

[Accepted 14th October 1958]

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INTRODUCTION

Three previous reports on the reptiles collected by Mr Ionides in Tanganyika Territory have been published (Loveridge, 1951, 1955 and 1957 a).

The present paper consists of comments on selected specimens submitted to me for study by Mr Ionides who, now in retirement like myself, is devoting his time to furthering our knowledge of Tanganyika's herpetofauna. This material is listed directly below the species name, together with the collector's field number, preceded by the letter I (for Ionides ; though this letter does not appear on the tag that is attached to each specimen). Where no specific material is listed, the remarks consist of the more important observations made by Ionides who, with characteristic generosity, is allowing me to publish them. In such instances any measurements given are his. The observations deal with breeding seasons, diet, methods of feeding, effect of venom, enemies, etc., etc.

Among items of outstanding interest is the finding, by Ionides, of the Western Green-Snake (*Philothamnus i. irregularis*) in southeast Tanganyika Territory which, via the Zambezi, it may have invaded in recent years. The taking on Rondo Plateau of two *Crotaphopeltis werneri shrevei*, an Angolan tree snake new to East Africa, and the capture, near Kilwa, of the first authentic Parti-coloured Sea-Snake (*Pelamis platurus*) to be recorded from the coasts of British East Africa.

Also included are some notes made on the cotypes of the rarest of Tanganyika geckos (*Phyllodactylus wolterstorffi*) with a key to the African members of that genus ; some observations by Colonel M. W. Prynne on his rediscovery of the Kenya Hornless Chameleon (*Chamaeleo fischeri excubitor*). My reasons for suggesting a rearrangement of the lacertid genera of East Africa, together with a diagnostic key and table to facilitate their identification.

With the solitary exception of the *Crotaphopeltis* mentioned above, full citations of all species mentioned, together with type localities and synonyms, will be found in (Loveridge, 1957 b) so there seems no reason to repeat them here.

LOCALITIES FROM WHICH MATERIAL WAS COLLECTED

For convenience the localities from which material was procured is listed below, with the letters K.C. signifying Kenya Colony, and T.T. for Tanganyika Territory.

Arusha, 4,416 feet, Northern Province, T.T.
Kamweti, near Mt. Kenya, Embu District, K.C.
Laikinoi, 7,500 feet, Mt. Meru, Northern Province, T.T.
Liwale, Nachingwea District, Southern Province, T.T.
Makata, near Liwale (which see).
Makote, Newala District, Southern Province, T.T.
Mangirikiti, near Liwale (which see).
Masoko, sea level, Kilwa District, Southern Province, T.T.
Mihuru, about 2 miles from Newala (which see).
Mkundi, near Liwale (which see).
Mombasa, 70 feet, Coast Province, K.C.
Mtene, 2,200 feet, Rondo Plateau (which see).
Nakingombe near Zinja, Kilwa District, Southern Province, T.T.
Nanguruwe, Newala District (which see).
Newala, Newala District, Southern Province, T.T.
Rondo Plateau, *ca.* 2,700 feet, Southern Province, T.T.
Tanga, 50 feet, Tanga Province, T.T.

SYSTEMATIC LIST WITH OBSERVATIONS ON THE SPECIES COLLECTED

GEKKONIDAE

PHYLLODACTYLUS WOLTERSTORFFI (Tornier)

Diplodactylus wolterstorffi Tornier, 1900, Zool. Jahrb. (Syst.) **13**, 584, fig. A : Tanga, Tanganyika, Territory.

Type (Berlin Mus.) Paratype (Mus. Comp. Zool. Harv.) Tanga.

Possibly the rarest of Tanganyika geckos, being still known only from the original "cotypes". In (Loveridge, 1947, p. 252) *wolterstorffi* was still in the genus *Diplodactylus*. Later the researches of Garth Underwood (1954) restricted *Diplodactylus* to Australia. In 1956, through the kindness of Dr Hans Wermuth I was able to examine the eyes of Tornier's cotypes, one of which is now designated the type, and found they possessed the *Gekko*-type of pupil—i.e. vertical but with the lateral edges lobed—so transferred *wolterstorffi* to *Phyllodactylus* (as redefined by Underwood) (Loveridge, 1957 b, p. 189).

At that time I observed several minor discrepancies in Tornier's description, and as *wolterstorffi* is so very closely related to *Phyllodactylus inexpectatus* (Stejneger) of the Seychelles it seems advisable to publish the notes that I made by direct comparison of these scarce geckos, unrepresented in the collections of most museums.

In *wolterstorffi* the longitudinal diameter of the ear-opening is not quite (type) to one-third (paratype) the orbital diameter ; rostral pentagonal (type) or possibly septagonal (paratype), its superior concavity being slightly more accentuated than in *inexpectatus* (M.C.Z. 49108) whose rostral is quadrilateral ; upper labials 11–11 (type), 9–10 (paratype), 10–10 in *inexpectatus* ; lower labials 9–9 (type), 8–10 (right and left of paratype), 10–9 in *inexpectatus* ; mental *slightly* larger than adjacent labials (type), subequal (paratype), much larger in *inexpectatus* ; 12 undivided lamellae under fourth toe, breaking

up into small granules just before the digital expansion (type), 10 (paratype), in *inexpectatus* the 12 lamellae extend right up to the digital expansion though apparently this was not the case in the type ; digital expansion 1/2 (*not* 2/3rds) the orbital diameter (type), almost 2/3rds (paratype), 1/2 in M.C.Z. *inexpectatus* ; 3 (*not* 2) enlarged granules on either side beneath base of tail (type and paratype), 2 in *inexpectatus*, which has 6 lamellae on tip of tail.

In *wolterstorffi* the colour is somewhat bleached, but neither in the type or paratype is there any sign of a pale band from nostril through eye to above ear-opening ; tail pale grey with broad, though ill-defined, brown bands edged posteriorly with a single row of white scales (type) ; no banding on tail of paratype. This is in contradistinction to the M.C.Z. *inexpectatus* which is pale brown with about nine paired sepia blotches on either side of the vertebral line.

Total length of the *wolterstorffi* type, 110 (51+59) mm., of paratype, 105+ (57+48+) mm., the tail being regenerated ; length of *inexpectatus* (M.C.Z. 49108), 71 (37+34) mm. the tail presumably regenerated.

Careful consideration of the foregoing characters, combined with those given by Stejneger in his original description of *inexpectatus*, makes one wonder whether *wolterstorffi* is really distinct ? Could the cotypes have been brought from the Seychelles to Tanga with plants destined for that seaport or the nearby arboretum at Amani? The only apparent differences are those listed below. I have availed myself of the opportunity to include the only other African members of the genus known ; of these I have not seen *weileri* Müller.

Key to the African species of *Phyllodactylus*

1. Anterior row of postmental scales very large ; tail cylindrical ; range : East Africa ..... 2.
   Postmental scales more granular ; tail *Holaspis*-like, depressed and almost fringed laterally ; range : West Africa ..... 3.
2. Rostral quadrilateral ; a pale stripe from nostril through eye to above ear-opening ; range : Seychelle Islands ..... *inexpectatus*.
   Rostral pentagonal or even septagonal ; no stripe from nostril through eye to above ear-opening ; range : Tanga, Tanganyika Territory .... *wolterstorffi*.
3. Eyelid broad, some small conical tubercles among the scales on its upper part ; seven ventral scales in an area 2 mm. in length ; a dermal fold on posterior aspect of hind limb ; intertigital skin strongly developed, weblike ; range : British and French Cameroons ; French Congo..... *palmatus*.
   Eyelid narrow, covered with small uniform scales ; ten to eleven ventral scales in an area 2 mm. in length ; a slight fold on posterior aspect of hind limb ; interdigital skin scarcely developed ; range : British Cameroon ..... *weileri*.

CHAMAELEONIDAE

CHAMAELEO BITAENIATUS BITAENIATUS Fischer

Two females (I 7671 ; 7677) Laikinoi, 7,500 feet, viii, 57.

The larger, measuring 169 (92+77) mm., holds an infertile ovum and twelve unpigmented embryos ; the smaller, 160 (85+75) mm., ten pigmented foetuses measuring about 49 (28+21) mm. and apparently ready for deposition.

A coccinellid beetle, lygaeid bug, and a spider were recognisable among the much-chewed stomach-contents.

CHAMAELEO MELLERI (Gray)

One female (I 7885) Mtene, 23. i. 58.

This juvenile Giant One-horned Chameleon, measuring 290 (10+138+142) mm., was recovered from the stomach of a female *Crotaphopeltis w. shrevei* Loveridge. Ionides writes that a huge bulge in a Green Mamba (*Dendroaspis angusticeps*), captured alive at Mihuru on 1. i. 58, may also have been due to the presence of a *melleri*, for he took twenty-two of these chameleons between 26. xii. 57 and 10. i. 58 in the vicinity. Some were low in trees, others in bushes, a few on the ground. On previous occasions—and he had visited Newala Boma at all times of the year—these giant chameleons had always been observed only upon the higher branches of cashew and mango trees.

CHAMAELEO FISCHERI EXCUBITOR Barbour

During the Mau Mau troubles Colonel M. W. Prynne, when stationed near Mount Kenya, secured a number of these chameleons. Not only were they the first Kenya Hornless Chameleons to be obtained since the male was described in 1911, but he obtained examples of the previously unknown female. Writing me on 25th June 1956, Colonel Prynne remarks that the scalation of female *f. excubitor* is similar to that of the male, but her head is smaller and less rugged, her body deeper and more hunched, her limbs more slender, her tail thinner. In life the colouration of males ranged from buff (at night), through khaki, greenish brown, greenish sepia, reddish brown, reddish sepia to a purplish sepia.

In captivity " these lively little chameleons " do well. They are quick to hide on the far side of a branch (hence " *excubitor* " ?). Though they dislike being handled they become tame enough to take food from the fingers, rejecting maggots, mealworms and some kinds of beetles which other species of chameleons take readily. They partook freely of water held out to them on the end of a glass dropper. *C. f. excubitor* appear to be more tolerant of a wide temperature range than does *C. jacksonii*. Unlike *C. bitaeniatus höhnelii*, being of a peaceful disposition, they get along well in confinement with chameleons both of their own or other species. Unfortunately *siafu* (i.e. soldier ants of the genus *Dorylus*) attacked one night, killing seven males and a female, but two males, which Col. Prynne left at the British Museum in November 1955, respectively survived until April and June 1956.

CHAMAELEO FISCHERI TAVETANUS Steindachner

Male (I 7650) Arusha, 5,000 feet, viii 57.

This fine male, measuring 210 (10+90+110) mm., formed one of a series collected for Mr Ionides by Colonel J. Minnery.

CHAMAELEO JACKSONII JACKSONII Boulenger

Newly-born young, some in embryonic membrane, others just emerged.

Their mother was a hornless female taken at the edge of Mount Kenya forest near Kamweti, Embu District. For these specimens, now in the Museum

of Comparative Zoology, and the following notes, I am indebted to the donor, Colonel W. M. Prynne.

These chameleons formed part of a family of thirty-seven young, born at intervals of from two to four minutes on 12. i. 1954. Following parturition a few failed to rupture their natal embryonic membrane which soon dried and imprisoned the occupants. The majority, however, remained quiescent for periods of from ten to twenty seconds after which by means of convulsive movements they broke free. When freed these young made hostile displays at each other, but their mother showed no interest in them nor exhibited the slightest cannibal tendencies.

Hornless females are less common than those exhibiting at least some rudiments of horns, the rostral is almost invariably better developed than either of the orbital horns. Both horned and hornless females occur at Meru, Mount Kenya, for it was from this locality that Lönnberg (1911, K. Svenska Vetensk.-Akad. Handl. **47,** p. 20, pl. i, figs. 1–2) figured a hornless female. Horned females predominate, possible exclusively, at Nairobi, leading Tornier (1903, Zool. Jahrb., (Syst.) **19,** p. 176) to describe *C. jacksonii* var. *vauerescecae* as distinct. A contributory factor was the alleged type locality of *j. jacksonii*, erroneously given by Boulenger as " Uganda ", whereas it came from the Kikuyu country, possibly Nairobi, certainly from some point along the so-called " Uganda Railway " then under construction (cf. Loveridge, 1936, Publ. Field Mus. nat. Hist. Zool. Ser. **22,** p. 79).

More recent and conclusive confirmation of this variability is contained in an airletter from Col. M. W. Prynne, who writes on 15. xi. 1958 as follows : "Did I ever mention that the distinction between *C. jacksonii* and *C. j. vauerescecae* based on the horns of the female is clearly invalid ? I collected some fifty live *C. jacksonii* all from a small area just outside the forest on the south east side of Mt. Kenya. The females were all large adults and varied from those without any horns (just a pointed scale at the horn site) and others with single horns of various sizes, to those with three horns as in males but slender and flattish. Thus horns appear to be an entirely variable characteristic in the female and seem to be associated with secondary sexual characters. I noticed that the hornless females slept in the entirely female chameleon attitude—hunched with tightly coiled tail—while the fully horned female approached to some degree the male attitude, longitudinally extended. In fact the horned female seems to be rather like what farmers call a ' bully ' cow. Could this be an explanation of the behavioural variation ? "

The ovoviviparity of *C. jacksonii* and the half-dozen races of *bitaeniatus* may have been developed to combat the colder climatic conditions associated with the East African Highlands. Definite information is much needed as to the extent of its occurrence among the thirty-nine forms of chameleon (*Chamaeleo* and *Brookesia*) resident in East Africa. Spherical ova were frequently present when I reported on the state of the ovaries at various seasons in twenty-five of the forms, but the presence of even large, well-developed eggs is not conclusive evidence of a species being oviparous. Indeed, nothing less than observations of the female in the act of depositing her eggs.

This we know is done by members of the widespread, chiefly savannah-dwelling, *dilepis* group (embracing both *senegalensis* and *gracilis*). I have also found the buried eggs of the giant, single-horned *C. melleri*, and it appears certain that all seven species of *Brookesia* are oviparous—as the data obtained for four of them indicated.

BROOKESIA BREVICAUDATA (Matschie)

Ionides informs me that of this Bearded Pigmy-Chameleon (which I met with on the Rondo Plateau in 1939) he collected seven males and eight females at Mtene between 29. i and 21. ii. 58. In addition he procured four males and eleven females *B. brachyura ionidesi* Loveridge between 17. i and 24. ii. 58. Thus these two species appear to occur in about equal numbers in the same habitat, where they were sometimes found within a few yards of each other. Many were taken in pairs, the females holding eggs ready for deposition.

Ionides further observes that in life the colouration of *brevicaudata* has much green in its composition and is considerably brighter than that of *b. ionidesi*. The size, of course, was larger and the tail contained about three and a third times in total length. This of one male (I 7925) he measured, is given as 93 (65+28) mm.

SCINCIDAE

ABLEPHARUS BOUTONII AFRICANUS Sternfeld

At Masoko, Kilwa, Ionides collected and identified a small series of this Coral-rag Skink, which he presented to the Museum of Comparative Zoology (*circa* viii. 57).

CORDYLIDAE

GERRHOSAURUS MAJOR GRANDIS Boulenger

On 19th June 1957, an adult Zululand Great Plated-Lizard, basking outside a termitarium, sought refuge within it when disturbed. On learning of this, Ionides instructed his collectors to return and close every hole in the termitarium except one, at whose entrance they were told to set a "catch-it-alive" trap. Three days passed without anything being caught so Ionides dug out the hole. No lizard was encountered but they did find seven moist eggs, stuck end to end, each measuring about 14 × 37 mm. These eggs (I 7609) were subsequently sent to the Museum of Comparative Zoology (Kilwa : 22. vi. 57).

When digging out a halfgrown male *G. m. grandis* from an abandoned termitarium, a mongoose (*Herpestes ignitus*) bolted from another section of the same tunnel (Nakingombe, Zinga, Kilwa District : 16. xi. 57).

On 15th June 1957, one of Ionides' messengers was cycling along a footpath when he saw a *mwewe* (Kingindo name) or kite (*Milvus migrans parasitus*) rise from the ground with an adult female *grandis* in its talons. As the man accelerated towards the bird, the lizard, abandoning its tail, fell ; the kite then dropped the spiny tail (Makata : 15. vi. 57).

LACERTIDAE

Arrangement of the Genera of Lacertidae *occurring in East Africa.*

In Boulenger (1920, p. 2) *Nucras* was placed first in the belief that geologically it was the earliest known genus. This assumption, however, rested on a specimen that was almost certainly preserved in so-called " Zanzibar copal " and *not* in Baltic amber as originally supposed.

When I was engaged in compiling the " Check List of East African Reptiles " (Loveridge, 1957 b), considerable time was spent in endeavouring to discover an arrangement that would better reflect the relationships of the lacertid genera though, being based on external characters, I am fully aware that the result should be regarded as tentative pending comparative anatomical and osteological studies. However, for what they may be worth, I offer the following key and synoptic table. From these it will be noted that at least two of the first three genera are entirely arboreal ; *Algyroides* and *Lacerta* embrace semi-arboreal and semi-terrestrial forms in East Africa, while the last four genera are solely terrestrial.

The definitions of several of these genera are so similar that I used to have considerable difficulty in deciding to which genus a captured lizard should be assigned. Since my last attempt (Loveridge, 1923) to formulate a key to this group, two additional genera have been added to the East African herpetofauna.

Key to the Genera of Lacertidae in East Africa.

1.	Digits and tail with strong lateral serrations ; tail strongly depressed....	*Holaspis.*
	Digits not or but scarcely, and tail without lateral serrations; tail not strongly depressed	2.
2.	Ventrals keeled	3.
	Ventrals smooth	4.
3.	Dorsals small, juxtaposed, obtusely keeled.....	*Gastropholis.*
	Dorsals large, rhomboidal, imbricate, keeled	*Bedriaga.*
4.	Median dorsals in from two to six plate-like series	*Philochortus.*
	Median dorsals similar to the dorso-laterals	5.
5.	Underside of digits smooth or tubercular	6.
	Underside of digits keeled	8.
6.	Dorsals large, imbricate	*Algyroides.*
	Dorsals moderate or small, subimbricate or juxtaposed	7.
7.	Nostril surrounded by two or three nasals *and* a labial, or separated from the latter by a narrow rim	*Lacerta.*
	Nostril surrounded by two or three nasals only.....	*Nucras.*
8.	Nostril surrounded by three to five nasals and a labial, or narrowly separated from the latter ; collar strongly developed	*Latastia.*
	Nostril surrounded by two to four nasals, well separated from the labial ; collar more or less distinct, feebly marked or absent	9.
9.	Nostril surrounded by three or four nasals only ; dorsals small; collar more or less distinct	*Eremias.*
	Nostril surrounded by two or three nasals only ; dorsals rather large, rhombic or lanceolate ; collar feebly marked or absent	*Ichnotropis.*

Table of characters on which the Key to the genera of Lacertidae in East Africa is based

Boulenger position	Genus	Ventrals	Dorsals	Dorsals	Dorsals	Collar	Nasals around nostril	Digits serrated laterally	Digits smooth, tubercular, keeled
7	*Gastropholis*	Keeled	Obtusely keeled	Small	Juxtaposed	Strong	2 narrowly separated from labial	No	S
8	*Bedriaga**	,,	Keeled	Large, rhomboidal	Imbricate	,,	2+labial	No	S
22	*Holaspis*	Smooth	Median smooth, laterals S or K	2 median, plate-like series		,,	2 narrowly separated from labial	Yes	S
4	*Philochortus*	,,	Obtusely keeled	2–6 median plate-like series		,,	2, either narrowly separated from, or + labial	No	S or T
3	*Algyroides*	,,	More or less strongly keeled	Large	Imbricate	,,	2 or 3 as last genus	No	S or T
2	*Lacerta*	,,	Smooth or strongly keeled†	Small or moderate	Subimbricate or juxtaposed	,,	2 or 3 as last genus	No	S or T
1	*Nucras*	,,	Smooth or keeled	Small or moderate	Juxtaposed	,,	2 or 3	No	S or T
5	*Latastia*	,,	Smooth or keeled	Small or large	Imbricate or juxtaposed	,,	3 to 5 either narrowly separated from, or + labial	No	K
18	*Eremias*	,,	Smooth or keeled	Small	Subimbricate or juxtaposed	More or less distinct	3 or 4 well separated from labial	?	K
15	*Ichnotropis*	,,	Strongly keeled	Rather large, rhombic or lanceolate	Imbricate	Feebly marked or absent	2 or 3	?	K

* Connects *Gastropholis* and *Algyroides*.

† As amended in Loveridge, 1942. Bull. Mus. comp. Zool. Harv. **91**, pp. 333–334.

VARANIDAE

VARANUS NILOTICUS NILOTICUS (Linnaeus)

A female Nile Monitor, taken at Masoko Mission on 14. viii. 57, was fed on hens' eggs. Before taking one the lizard would first swallow a drink of water, then break the egg in her mouth. After eating the contents she proceeded to crunch and swallow the shell piecemeal. Subsequently this reptile was sent to Chester Zoo.

VARANUS EXANTHEMATICUS MICROSTICTUS Boettger

About 2.45 p.m. on 5th October 1957, Ionides captured the smallest monitor he has ever seen—she (I 7683) measured 234 (101+133) mm. Sent to the Museum of Comparative Zoology at Harvard, she was identified as *microstictus* by Dr E. E. Williams.

AMPHISBAENIDAE

ANCYCLOCRANIUM IONIDESI Loveridge

Three (I 7786 ; 7908 ; 7984) Mtene, 23. i.–19. ii. 58.

Nostril pierced in a nasal which anteriorly is fused with the enormous rostral ; 32 (16+16) to 34 (18+16) segments in a midbody annulus ; 298, 301 and 303 annuli on body ; 22, 23 and 22 annuli on tail. Total lengths 208, (190+18) mm., 214 (195+19) mm. and 235 (215+20) mm.

The finding of these Kilwa Sharp-snouted Worm-Lizards on the Rondo Plateau, not only doubles the number of known specimens but constitutes a noteworthy extension of their altitudinal range.

AMPHISBAENA RONDOENSIS Loveridge

One male, one female (I 7908 ; 7980) Mtene, 17–20. ii. 58.

These Nchingidi Worm-Lizards from the other end of the Plateau, possess the 10 dorsal and 10 ventral segments characteristic of the species, but in size surpass the type series of forty-nine specimens. Total length of male, 135 (119+16) mm., of female, 155 (138+17) mm.

TYPHLOPIDAE

TYPHLOPS TETTENSIS TETTENSIS (Peters)

Six (I 7782 ; 7789 ; 7796 ; 7798 ; 7853 ; 7861) Mihuru, 27. xii. 57.–13. i. 58.
Three (I 8043 ; 8323 ; 8335) Liwale, 11. iii.-26. iv. 58.

Midbody scale-rows 22 (at Liwale) or 24 (at Mihuru) ; midbody diameters included 37·2 to 45·5 times in total lengths of from 290 (285+5) mm. to 400 (396+4 mm.) (influenced by sex). Above, the light (greenish white) dorsal spots are situated on the *posterior* portion of each scale. Below, creamy white to yellowish green, flecked with dark grey-green except in two specimens (I 7789 ; 7853) which, in this respect, approach the colouring of *T. t. rondoensis*.

* Connects *Gastrophelis* and *Algyroides*.
† As amended in Loveridge, 1942. Bull. Mus. comp. Zool. Harv. **91**. pp. 333–334.

TYPHLOPS TETTENSIS RONDOENSIS Loveridge

Five (I 7871 ; 7877 ; 7891 ; 7982 ; 7992) Mtene, 19. i.–21. ii. 58.

Midbody scale-rows 22–26 (three were 24 ; extremes checked) ; midbody diameters included 35 to 46·8 times in total lengths of from 193 (190+3) mm. to 375 (370+5) mm. Below, white, uniform.

These Rondo Blind-Snakes were sent me by Mr Ionides to show that it is no longer possible to separate them from the typical form on the basis of midbody scale-rows. However, he goes on to say that he submitted this series from Rondo Plateau, together with those from Mihuru, near Newala, to a friend, who, without looking at the labels, but depending solely on the position of the light spot on each dorsal scale, unhestitatingly separated the *t. tettensis* into one pile, the *t. rondoensis* into another. Though this character is certainly useful, occasionally one finds the light spots on both the anterior and posterior ends of the scale in the same snake. There remains, therefore, the colouring of the undersurface as the only certain diagnostic character, though there are several average differences.

LEPTOTYPHLOPIDAE

LEPTOTYPHLOPS LONGICAUDA (Peters)

One male (I 8333) Liwale, 27. iv. 58.

Midbody diameter included fifty times, and tail ten times, in a total length of 150 (135+15) mm. Taken in a pile of decaying debris. Two other examples of the Long-tailed Flesh-pink Worm-Snake were subsequently taken in this locality by Mr Ionides.

COLUBRIDAE

BOAEDON FULIGINOSUS FULIGINOSUS (Boie)

Ionides reports that a male Common House-Snake, coiled about an adult House-Gecko (*Hemidactylus mabouia*), fell from the roof of a native hut. The prey was overcome and swallowed in about ten minutes (Liwale : 28. iii. 58).

Also, in some decaying debris at the edge of a muddy rice field, he came upon a quite moderately sized female with three coils round a shrew (I 8157 det. *Crocidura fumosa* at Chicago Nat. Hist. Mus. 148 mm. ; tail 84 mm. ; H.F. 14 mm. ; ear 7 mm.) whose head was held in the snake's jaws. So slender was the snake in relation to its prey that Ionides' African assistants would not credit the snake with being able to overcome and assimilate the mammal. However, violent though the shrew's struggles were at first, they gradually lessened, and in rather more than half an hour after the combatants had been found, the last vestige of the shrew's tail had disappeared. Skins of shrews collected in the same area the same day, have been sent for identification (Liwale : 23. iii. 58).

MEHELYA NYASSAE (Günther)

Two males (I 8311 ; 8320) Liwale, 23–24. iv. 58.

Midbody scale-rows 15 ; ventrals 167–169 ; anal 1 ; subcaudals 64–68 ; upper labials 7, third and fourth entering orbit. Total lengths 208 (167+41) mm., and 228 (180+48) mm.

As a comparably small juvenile was taken at Liwale on 21st April 1952 Mr Ionides suggests that late April may be the hatching season for this species in this area. Both these males were taken among rotting debris at the edge of mahoga gardens following a night of fairly heavy rain. The stomachs of both held Snake-eyed Skinks (*Ablepharus wahlbergii*). They were submitted by Ionides because males, especially juveniles, of this species are rare in collections.

PHILOTHAMNUS MACROPS (Boulenger)

One male, three females (I 7882 ; 7935 ; 7986 ; 7997) Mtene, 23. i.–24. ii. 58.

Midbody scale-rows 13 ; ventrals 138–142 ; anals 2 ; subcaudals 73–77 ; upper labials 8, the fourth and fifth entering the orbit except on left side of I 7986 where there are nine labials with the fifth and sixth entering.

These Usambara Green-Snakes were submitted on account of their unusual colouring. Not only are the two adult females brown above (as previously described for another Rondo Plateau female. (Cf. Loveridge, 1942, p. 271), but they have from 28 to 34 broad, black, wavy, more or less well-defined cross-bars, so that in colouration I 7882 bears a distinct resemblance to the local night adder (*Causus defilippii*). However, where scaling has taken place in alcohol, the underlying scales are of a greenish silver hue. One juvenile male (?) is pale to dark gray below (? olive in life) with two (right) to four (left) lower labials white ; there is a white blotch on each anterior sublingual and similar white blotches on the anterior ventrals, especially from the third to the eighth. The effect is very striking. In total lengths the females range from 187 (144+43) mm. to 604 (440+164) mm. The latter is the one whose colouration is described above, she holds seven eggs (I 7884) measuring *about* 12 to 13×25 mm. in alcohol. She was taken beneath some rubbish in a forest-surrounded *shamba* (native plot).

PHILOTHAMNUS IRREGULARIS IRREGULARIS (Leach)

One male, one female (I 8192 ; 8283) Mangirikiti, Liwale, 29. iii.–18. iv. 58.

Midbody scale-rows 15 ; ventrals 160–162 ; anals 2 ; subcaudals 96–111 ; upper labials 8 or 9, fourth, fifth and sixth entering the orbit ; preocular 1 ; postoculars 2; temporals 1+2, though a small scale is split off from the anterior temporal on both sides of I 8192. Length of male, 795 (530+265) mm., of female, 984 (690+294) mm.

The male was taken in a grove of bananas near water, the female in a low tree in a small thicket near Liwale River. The capture of these typical *irregularis* constitute the first records of its occurrence in southeast Tanganyika Territory ; in the northeast *P. i. battersbyi* Loveridge is common, but is unknown south of the Usambara Mountains.

CROTAPHOPELITS WERNERI SHREVEI Loveridge

Crotaphopeltis shrevei Loveridge, 1932, Proc. Biol. Soc. Washington, **45**, p. 83 ; Missao de Dondi, Bella Vista, viz. Lobito, Angola.

Two females adult & juvenile (I 7883 ; 7889) Mtene, 23–24. i. 58.

The finding of these arboreal snakes on Rondo Plateau by Mr Ionides, constitutes a noteworthy addition to the herpetofauna of Tanganyika Territory

which will not be found in the recent (1957) check list. The seeming gap in distribution is bridged by Dr H. W. Parker having reported *shrevei* from Northern Rhodesia, and Dr E. E. Williams writes me that he has also identified a juvenile collected there by Vesey-Fitzgerald. On comparing the description of *shrevei* with these two Rondo snakes, one observes only inconsequential differences which may be summarized as follows.

Frontal $1\frac{1}{4}$ (juv.) to $1\frac{3}{4}$ (ad.) as long as broad (across the middle), considerably (juv.) to slightly (ad.) longer than its distance from end of snout ; loreal of juvenile slightly (left) to markedly (right) higher than broad ; temporals 1+1 (ad. and right side of juv.) or fused (left side of juv.) so that the resulting very elongate scale might be called 1+2 ; behind the well-developed sublinguals are from 4 (ad.) to 6 (juv.) ordinary scales resembling the sublabials. On neck at a distance of ten scales behind the parietals the scale-rows number 19 or 21 (instead of 23) ; ventrals 207–210 (203 in male type) ; anal single ; subcaudals 95–96 (81 in male type).

Colour of adult female in alcohol. Above, uniformly grey (olive in life, writes Ionides). Below, white, uniform, except for the outermost borders of the ventrals and subcaudals on which the dorsal colouring impinges progressively towards the tip of tail—so that much of the latter is dusted with grey. Colour of juvenile female in alcohol. Above, pale brown, lighter on flanks. Below, white, uniform except for the centre of each subcaudal being brownish.

Total length of female juv., 276 (215+61) mm. ; of adult female, 1025 (790 + 235) mm. The latter had recently swallowed a $11\frac{1}{2}$ inch *Chamaeleo melleri*, an astonishing meal for this relatively slender snake, and fell from a tall tree.

It appears advisable to regard *shrevei* as a subspecies of *werneri* Boulenger (1897) as these Rondo snakes differ from that species, apart from colouration, in characters that appear to be more or less of an intermediate nature, viz.

The description of *werneri* calls for a rostral " scarcely visible from above ", possibly a matter of interpretation as it is clearly visible in both Rondo snakes ; in the juvenile the loreal agrees with *werneri* in being " deeper than long " on one side of the head only, being longer than deep on the other and in the adult ; through fusion the temporals are 1+2 on left side of the juvenile but 1+1 on the other and in the adult (1+2 in *werneri*, *reticulatus* and *shrevei*). *Dipsadomorphus reticulatus* Werner (1909) was referred to the synonymy of *werneri* by Boulenger, correctly I think, though they differed considerably in colour pattern.

These differences may be synopsized as follows :

Ventrals 203 (Angola male) to 207–210 (Rondo females) ; subcaudals 81 (Angola male) to 95–96 (Rondo females) ; colour (of juv.) above, pale brown (of ad.) olive, grey or blue-black, uniform ; belly white, uniform (juv.) or anteriorly with the dorsal colouring impinging progressively laterally on ventrals until the white is almost obscured posteriorly (ad.) ; subcaudals dusted with brown (juv.), or grey, or wholly plumbeus (ad.). Range : Angola east through Northern Rhodesia to southeastern Tanganyika Territory *w. shrevei*.

Ventrals 219–225 (Usambara and Tanga, unsexed) ; subcaudals 101 (tail-tip missing in type of *reticulatus*) ; colour (of juv.) above, anteriorly grey-brown uniform, posteriorly with dark spots that tend to coalesce and form cross-bands, or (of ad.) above, snout and much of head grey-brown, rest of dorsum bright yellow-brown with bases of the scales and interstitial skin black ; belly (of juv.) ventrals yellowish white with the dorsal colouring usually impinging laterally ; or (ad.) below having throat and anterior ventrals yellowish, posterior ventrals bordered and broadly margined with dark grey ; subcaudals brown (juv.), or from three-quarters to all of each dark grey, the rest a lighter grey. Range : Usambara Mountains and Tanga, northeastern Tanganyika Territory ..... *w. werneri.*

One might add that in the foregoing synopsis of *werneri*, " juvenile " refers to the 370 (285+85) mm. type from the Usambara Mountains, " adult " to the 1280+ (1010+270+) mm. type of *reticulatus* from Tanga (which formerly fostered virgin forest akin to that of the Usambara).

AMBLYODIPSAS KATANGENSIS IONIDESI Loveridge

One female (I 7962) Mtene, 11. ii. 58.

Midbody scale-rows 15 ; ventrals 195 ; anal divided ; subcaudals 19 ; postocular 0. Below, irregularly chequered black and white. Total length 405 (379+26) mm. ; consequently this appears to be the largest known female. The locality also constitutes an extension in the known range of this subspecies.

ELAPIDAE

ELAPSOIDEA SUNDEVALLII DECOSTERI Boulenger

At Mkundi, Liwale, on 17th May 1957, Mr Ionides found a pair (male and female) of Southeastern Garter-Snakes in close proximity beneath some rotting vegetation at the edge of a *shamba*. They were placed in separate bags until camp was reached about noon, then they were transferred to a box containing other reptiles—including a fairly large *Psammophis subtaeniatus sudanensis* captured the day before. This sand-snake, upon the introduction of the male garter-snake, began thrashing about and was twice bitten by the garter-snake in the lower back ; on both occasions the garter-snake held on and chewed. Anticipating the early demise of the sand-snake, Ionides removed her to a bag, but at 8 a.m. on the following day she appeared lively and well, showing no symptoms of poisoning even at the sites where she had been bitten. The garter-snake disgorged a freshly-swallowed banana-frog (*Afrixalus b. brachycnemis*) when he was captured, but was not seen to expend its venom in biting anything.

NAJA NIGRICOLLIS NIGRICOLLIS Reinhardt

A recently-hatched male spitting-cobra was taken near Mihuru on 25. xii. 57 by Ionides.

NAJA MELANOLEUCA Hallowell

Ionides writes that within 200 yards of where he took a typically black *melanoleuca* in May, 1945, he has just captured a fine adult male of the brown form described as *fulva* by Laurent in 1955. This leads him to question the significance of the latter. It seems to me, however, that Ionides may well

be operating in an area where the two forms meet. Ionides adds that he had been looking for this particular snake for three days, having observed that Black-and-White Cobras are apt to take up residence in a particular place and remain there for some considerable time (Liwale : 11. vi. 58).

DENDROASPIS ANGUSTICEPS (Smith)

Two recently-hatched females of the Common Green Mamba, the smaller (I 7783) measuring about 424 (321+103) mm., were taken near Mihuru on 26 and 27, xii. 57 by Ionides.

DENDROASPIS POLYLEPIS POLYLEPIS Günther

At Makata, near Liwale, about 6 p.m. on 23. iv. 57, Ionides was walking along a motor road when a female " Black " Mamba emerged from the grass on the left and began to cross. On catching sight of Ionides and his companion she raised her head about two feet from the ground and took a good look at them, then, turning aside, continued slowly on her way. Stepping forward, Ionides pinned her to the ground about midbody—he estimated her length as about 7½ feet. On feeling the pressure of the stick she turned upon him. Ionides remarks that on previous occasions he has observed similar indifference to men exhibited by the larger elapids.

HYDROPHIIDAE

PELAMIS PLATURUS (Linnaeus)

One male (I 7610) Masoko near Kilwa, 27. viii. 57.

Though this Parti-coloured Sea-Snake was included in my check list, published in August, 1957, I rightly stated that I knew of no definite capture of this species on the East African coast. No sooner was the check list published than C. J. P. Ionides proceeded to render it out of date by collecting this fine specimen ! He found it still alive, though in moribund condition, among some seaweed in a foot of water retained by the coral rag. The tide had just turned and was coming in about 12.30 p.m. when his long search was rewarded.

Midbody scales 64 ; scales between sublingual and anal about 328 (of which rather less than 28 might be considered gulars).

So numerous are the colour variants of this widely distributed species that it is as well to record the markings of this historical individual. Above, crown of head black merging into a broad, slightly convergent (twenty scales wide on nape, narrowing to twelve at a point about 50 mm. anterior to anus), black vertebral band, that is straight-sided until 50 mm. before anus when it is indented by the lemon yellow colouring of the flanks, precursor to six saddle-shaped black patches on upper edge of tail, the latter being irregularly blotched with black on its sides and below. Sides of jaws flecked with yellow, throat yellow or brown ; right flank mostly lemon-yellow with some brown flecking ; on left flank only the anterior quarter mostly yellow, thereafter the yellow persists as a more-or-less well-defined lateral band about five scales in width, the lower flank and belly being brown.

Ionides writes that in life, apart from the black and yellow markings, most of the body was dull green, but the snake was about to slough and when some of the epidermis came away in alcohol the scales underlying the dull green were seen to be yellow.

Total length of male, 693 (625+68) mm.

On neck and flank are two small sores which look as if parasites might have escaped from their central apertures ; on either flank posteriorly near anus are healed wounds which might have been caused by a bite.

Captain H. L. Holland of R.M.S. " Braemar Castle " informed me (A. L.) today (30. ix. 57) that several months ago at Mombasa a customs or other official picked up a sea-snake, believing it to be dead, in order to photograph it. The snake bit its captor, who then drove to Mombasa Hospital where he collapsed. It was found necessary to amputate his arm. However, in reply to my request for corroboration of this incident, Dr L. S. B. Leakey of the Coryndon Museum, Nairobi, informs me that the snake was eventually identified as a young Puff Adder (*Bitis a. arietans*) that, presumably had wandered on to the shore to bask.

VIPERIDAE

CAUSUS DELILIPPII (Jan)

An unusually large male, about 441 (406+35) mm., taken with a female, about 445 (420+25) mm., which held fifteen eggs, each measuring about 13×21 mm., was collected and measured at Mihuru by Ionides 29. xii. 57.

BITIS ARIETANS ARIETANS (Merrem)

A female which Ionides had had in captivity since early July, gave birth to thirty-two (9 males, 23 females) young at Mihuru on the night of January 6th to 7th, 1958. He measured one new-born male as about 191 (167+24) mm., and a female as about 181 (168+13) mm.

BITIS GABONICA GABONICA (Duméril & Bibron)

One male (I 7873) Mtene, 20. i. 58.

Midbody scale-rows 36 ; ventrals 131 ; subcaudals 24^{+}? This juvenile, unlike some other *gabonica* recorded from Rondo Plateau, exhibits the markings of the typical form ; the large black temporal patch extends forwards to the subocular region but is bisected by a fine light line connecting the orbit with the ninth labial. Ionides writes me that a juvenile female, taken on the 17th, was similarly marked. Also that the dark temporal patch was divided by a white line in two Mihuru vipers, the male taken 9. iii. 57, the female on 12. iii. 57.

Between 16th June and 21st July, 1958, locally the cool season and apparently the best time of year to look for Gaboon Vipers, Ionides caught twenty-one of these big snakes. Three were found at Makote and eighteen near Nanguruwe. The largest, taken on 17th July, was an adult female weighing 11½ lb. Despite her size she offered little resistance to being placed in a box when captured, nor the following day when transferred to a travelling

bag in preparation for a journey by air to the Coryndon Museum for casting. Ionides found even *Bitis nasicornis* more inclined to bite than *gabonica*, which he regards as the most good natured of all the highly venomous snakes of his acquaintance.

About 10.15 a.m. on 19th July, in some bushes in a cashew-tree plantation at Nanguruwe, Ionides took a young female *gabonica* some two feet in length. Observing a feather adhering to the right side of her mouth, Ionides forced her to disgorge a recently swallowed bird about the size of a thrush, though unidentifiable owing to its condition. Here was concrete evidence that this normally mammal-eating snake will, on occasion under natural conditions, take a bird. This lends support to the repeated assertions of local Makonde and Makua tribesmen that Gaboon Vipers sometimes devour their young poultry.

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Early tusk development in a ycung African elephant shown in the young elephant on the extreme right.

AN APPARENT CASE OF PRECOCIOUS TUSK GROWTH IN A YOUNG AFRICAN ELEPHANT

BY

C. A. SPINAGE, F.Z.S.

c/o E.A.A.F.R.O., Kikuyu, Kenya.

[Accepted 14th October 1958]

(With 1 plate)

Morrison-Scott (1947) summarises the evidence concerning " pygmy " elephants finishing with the words, " . . . there is a good deal of confusion due to the application of the word " pygmy " to forest elephants and there is plenty of wishful thinking, but there is as yet no good evidence of a real pygmy elephant ".

Although presumably " pygmy " elephants have been classed as such on account of their possessing relatively large tusks for their size, there appears to be a dearth of recorded measurements of the tusks of such elephants.

The accompanying photograph was taken by the writer in the Queen Elizabeth National Park of Western Uganda in June 1956. The equipment used was a 240 mm. telephoto lens on a 6×9 cm. format, and the print is an enlargement of a small part of the negative.

It will be observed that the young elephant on the extreme right of the picture appears to have abnormally long tusks for its size. By simple measurement they seem to be almost as long as those of the large elephant running in the centre of the picture, whereas the tusks of the young elephant by the latter's side, which is almost the size of the elephant in question, are only just protruding. In the elephant standing by the side of the elephant in question the tusks are barely visible, and yet it is doubtful if there is more than a year's difference in their growth.

When the photograph was taken the elephants had been alarmed by a noisy motor car to the far right. The writer viewing them only through the camera view-finder did not notice the abnormality until the photograph was printed.

In the author's opinion the young elephant in the right of the photograph shows an abnormally long tusk growth for its size and aptly demonstrates how " pygmy " elephants probably get their name.

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OBSERVATIONS ON THE ST. KILDA FIELD-MOUSE *APODEMUS SYLVATICUS HIRTENSIS* BARRETT-HAMILTON

BY

J. MORTON BOYD

The Nature Conservancy, Edinburgh *

[Accepted 14th October 1958]

(With 1 plate and 3 figures in the text)

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INTRODUCTION

These observations on the St. Kilda field-mouse continue the work done in 1931 by Harrisson & Moy-Thomas (1933), in 1938 by Atkinson (1949), and in 1955 by the author (Boyd, 1956). They were made on three different visits to St. Kilda: 21st to 28th June 1956, as a member of the Glasgow University Expedition; 17th to 30th April 1957 and 7th to 14th June 1957 as the representative of the Nature Conservancy. At the request of the author observations were made between 5th and 23rd August 1957 by Mr Kenneth Williamson, the Warden of the St. Kilda Nature Reserve at that time, and between 29th November 1957 and 19th February 1958 by Dr R. P. Saundby, the Medical Officer of the Royal Air Force winter garrison on the island.

In mid-April 1957 an R.A.F. task force landed on St. Kilda. Between then and mid-September this task force, consisting of about 300 officers and men, constructed a camp, most of which was tented, in the lower meadows of the village. A road was built from this camp to installations near the summits of Mullach Mor and Mullach Sgar. The sudden incursion of the task force into the village area, which had not been inhabited for twenty-seven

* 12 Hope Terrace, Edinburgh 9.

years, was expected to cause disturbance to the population of St. Kilda field-mice (*Apodemus sylvaticus hirtensis* Barrett-Hamilton). This population was known to be dense in the locality of the camp. (Boyd, 1956 and results of the 1956 survey, see below.)

Close co-operation between the R.A.F., the Nature Conservancy, and the National Trust for Scotland (owners of St. Kilda), resulted in practically all of the dry-stoneworks which form an important part of the field-mouse habitat, being saved. As part of the plan to conserve the field-mouse at the beginning of the operations of the task force, the author conducted a widespread survey in Hirta to obtain an idea of the density pattern throughout the island. Further trapping was done in June and August to assess the damage, if any, done by the presence of the task force.

Data giving the distribution of weights of mice caught in April, May, June, July, August, December-January, February, and March are now available, together with information on the descent of the testes and perforation of females. From these figures the reproductive cycle of the St. Kilda field-mouse can be outlined.

METHODS

Work performed in 1956

The 1956 survey was a repeat of those in 1955 and 1931. It took the form of a transect through the meadows from the storm beach to the perimeter wall, below and above the village street between the Factor's House and Cottage 1 (Fig. 1). The R.A.F. camp was subsequently built across this transect line in 1957.

Twenty " Longworth " traps were set in groups of five at the same stations each day. The traps were spaced at intervals of ten metres. The stations were as follows: (i) immediately behind the storm beach, (ii) lower village meadows along the Dry Burn, (iii) the line of the village street, (iv) the perimeter wall inside the village enclosure (Fig. 1). The traps were kept in the same position for the first five days, and moved to a new position in the same stations on the last two days. The traps were baited with rat diet No. 41, as in 1955, and prebaiting was not done. They were set in the afternoon and cleared on the following morning. The mice were weighed, marked and released at the trap-site where each was caught.

Work performed in 1957 *and early* 1958

In 1957 the same bait was used as in 1955 and 1956 but in February 1958 crushed biscuit was used instead. The traps were not prebaited and were set and cleared on consecutive afternoons and mornings. The mice were weighed and released at the point of capture. In some cases individuals were anaesthetised and both ecto and endoparasites obtained.

The field-mouse population in the village area is closely associated with the dry-stoneworks of walls, cleitean (dry-stone storage chambers) and houses—see Boyd (1956)—and this was taken into account when choosing a sampling unit. The cleitean, or " cleits " widely scattered throughout the island (see Plate) were used as trap-sites; there the largest local aggregations of mice

might be expected, and by setting the traps inside the cleitean the effects of changes of weather, particularly rain, were minimised.

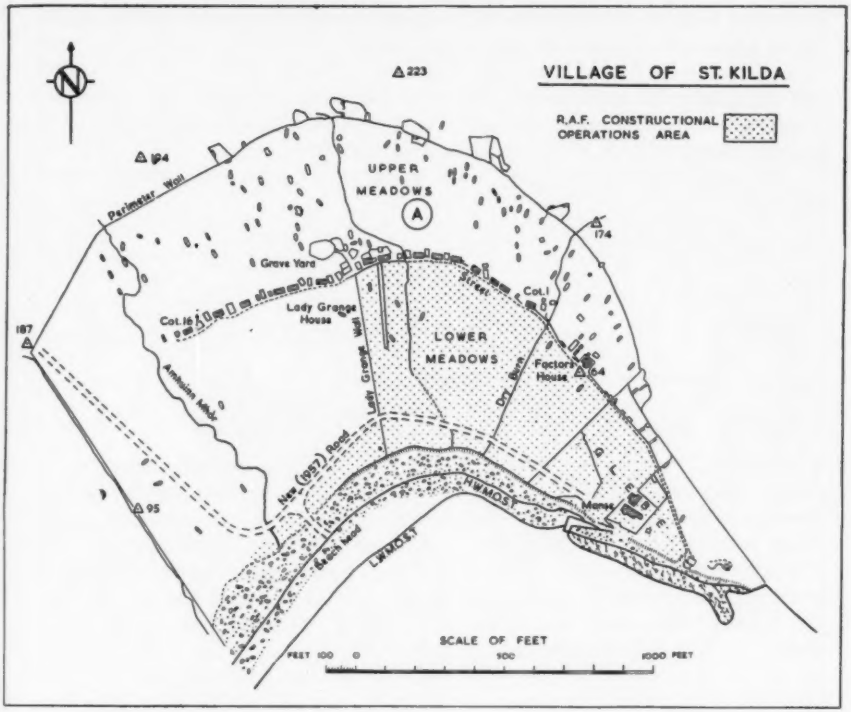

Fig. 1.—Map of the village area, Hirta, St. Kilda showing area of constructional operations during 1957-58.

Groups of five neighbouring cleitean were chosen in thirty localities of Hirta (Fig. 2), and two traps were set in each, one at each end in a position where sheltering sheep would not kick them over. Widely-separated groups of cleitean were chosen to reduce the chances of catching the same mouse twice.

In the analysis of the results it was necessary to distinguish adults and juveniles. In February and April, when the entire population was probably adult, mice of less than 25 gm. were not caught. It was thus decided to consider as adults all mice heavier than 25 gm.

TRANSECT OF 1956

The weather during the period 21st to 28th June, was consistently fair with winds from the NW. The results are given in Table 1. Sixty-one mice were trapped in 140 trap-nights, and two escaped before examination. Of

the 61 there were 37 different individuals and probably 26 of them were adult. At about the same four stations in May 1955, 49 mice were caught in 80 trap-nights; 28 were different individuals and probably all were adult. The difference between 61 mice in 140 trap-nights and 49 mice in 80 trap-nights (44 as against 60 per cent success) is significant ($\chi^2=6{\cdot}365$), but that between 37 different mice in 140 trap-nights and 28 different mice in 80 trap-nights (26 as against 35 per cent) is not significant ($\chi^2=1{\cdot}801$). The difference between 26 adults in 140 trap-nights and 28 adults in 80 trap-nights (19 as against 35 per cent) is highly significant ($\chi^2=19{\cdot}033$).

All probabilities in this paper are taken at the 0·05 level, except where stated.

Fig. 2.—Map of Hirta showing the stations at which trapping was carried out.

TABLE 1

Success by five traps each night at each station. Male/Female sex-ratios are given beside the totals.

Date June 1956	Stations 1	2	3	4	Total (1–4)
21–22	1	3	0	1	(2/3) 5
22–23	5	3	1	3	(10/2) 12
23–24	3	2	3	3*	(7/3) 11*
24–25	2	4	0	3	(8/1) 9
25–26	1	2	1	1	(4/1) 5
26–27	3	3	2	3	(5/6) 11
27–28	2*	2	1	3	(6/1) 8*
Total (1–4)	(9/7) 17*	(16/3) 19	(7/1) 8	(10/6) 17*	(42/17) 61**

*=one mouse escaped before sexing.

Do these differences indicate a change in numbers in the period 1955–1956 ? In May the population (excluding nestlings) was composed of adults. Fewer adults might be expected because of mortality and temporary lack of replacement by maturing juveniles. It is doubtful, however, if this alone could account for such a difference in adult strengths. There are a few transient predators, a few resident ravens and crows and no competition with other small mammals. Catches of St. Kilda field-mice are, in the experience of the author and Harrisson & Moy-Thomas (1933), greatly affected by the weather, but this could scarcely have been responsible for the difference between the 1955 and 1956 catches, since on both occasions the weather was consistently fair. The fact that there are more juveniles in June than in May could have reduced the catch of adults by traps being tenanted by juveniles when visited by adults. One would expect the total population to be greater in June than in May; the results, however, do not show this and it is probable that mice were more numerous in 1955 than in 1956. Numbers during those years, however, were of the same order and much greater than in 1931. The reasons for this great change are discussed by Boyd (1956), and is connected with the evacuation of domesticated cats and dogs.

Of the 37 individuals trapped, 12 were females (7 adults) and 25 males (19 adults). Of the 11 juveniles, five were female. One adult female and nine adult males were retrapped. Three female and three male juveniles were retrapped. Many more adult males than females were retrapped which is contrary to the results of May 1955 when the opposite was the case. This does not substantiate the suggestion (Boyd, 1956) that the trapping may be sex-selective. In June some adult females (as Hacker & Pearson (1944) also found) were probably nursing, and this may well have affected their movements and behaviour.

SURVEY OF 1957

Density pattern on Hirta

The results of the survey conducted between 17th and 30th April 1957 are set forth in Table 2. Throughout the period the weather varied greatly.

TABLE 2

The results of trapping at 30 stations throughout Hirta; 10 traps set at each in a group of five neighbouring cleitean, one trap at both ends of each cleitean.

Station Number	Station	Height above H.W.M.O.S.T. (feet)	Total Wt. trapped (gm).	Mice trapped
1	Low. Amhuinn Mhor	70	169	5
2	Up. Amhuinn Mhor	160	160	4
3	Behind graveyard	160	79	3
4	Behind cottage 5	120	120	4
5	Behind Factor's House	100	252	8
6	Behind Manse	50	267	8
7	Village " street "	95	233	8
8	" L. Grange cleits "	80	256	8
9	Lag Aitimir	340	118	3
10	Creagan Breac	380	36	1
11	An Lag Bho'n Tuath	260	118	3
12	Mullach Sgar	810	36	1
13	Mullach Geal	1050	0	0
14	Claig. na Tigh Faire	950	67	2
15	Carn Mor	500	154	4
16	Amazon's House	260	126	4
17	Gleann Mor (North-west)	200	25	1
18	Tobar Childa	195	172	5
19	Conachair (S.E.)	550	149	4
20	Oiseval (Summit)	900	0	0
21	Conachair (W. Summit)	1250	35	1
22	Clash na Bearnaich	110	245	7
23	The Gap	600	0	0
24	Mullach Mor (Summit)	1184	28*	2*
25	Gearaich Ard	280	60	2
26	Gleann Mor (Mid-floor)	325	97	3
27	Gleann Mor (Upper-floor)	450	37	1
28	Am Blaid	740	36	1
29	Oiseval (West Slope)	440	37	1
30	Behind storm beach	25	338	9

*=one escaped before weighing.

There were NW gales with heavy rain and hail, light to moderate SW winds with occasional showers, and calm bright spells lasting several days. The setting of the traps in the interior of the cleitean, however, seemed to reduce the effect of variable weather on the catch. On 18th and 19th April in fresh to strong NW winds with comparatively low temperatures and intermittent rain, 16 mice were caught in 20 traps set beside the Manse and Factor's House.

On the following day in warmer and drier weather the same number were caught from 20 traps set along the village street in the vicinity of Lady Grange's House (the locality probably having a somewhat similar population to that of the Manse and Factor's House area). Had the traps been set in the open, these catches would probably have been significantly different.

It was not possible to cover the whole island (Fig. 2). Gob na L-Airde, the Cambir, Ruaival, and all the cliff terraces with the exception of Carn Mor did not possess the necessary number of cleitean to give a standard sample (five cleitean with two traps in each). The results obtained from the areas trapped, however, show that the field-mouse is ubiquitous in Hirta in spring with the possible exception of inaccessible cliff-ledges, and, of course, precipices. Catches on the Carn Mor boulder-field would probably not have been significantly different if the traps had been placed in the recesses in the talus instead of in the interiors of the very small cleitean there. It is probable that comparatively dense aggregations of mice occur on other talus slopes without cleitean; this is particularly the case at Geo na Stacan, Mol Carn na Liana, and Ard Uachdarachd which like Carn Mor possess large nesting colonies of puffins (*Fratercula arctica*). Other talus slopes at Glacan Conachair and Clash na Bearnaich do not possess bird colonies and no doubt have smaller aggregation of mice than those already mentioned.

The largest catches were obtained in the vicinity of the village street and immediately behind the storm beach. The smallest catches were obtained on the exposed ridges. In Table 3 the island is divided into four regions for the purpose of comparing densities. The lowest number of samples obtained from any one region was four (from Gleann Mor) (1 sample = 5 × 2 traps),

TABLE 3

Four samples of 10 traps each (4 × 10 trap-nights) taken from four ecologically different areas of Hirta.

Area	Number of mice caught
Village area	25
Slope above village	13
Ridges	1
Gleann Mor	9

and four of the eight or nine obtained in the other regions were randomly chosen. The area inside the perimeter wall has the highest density and here the population was probably twice as dense in April as on the slopes above the village up to the 500 feet contour, and as in Gleann Mor. The population on the high ridges is probably more than 20 times less dense than in the village area, though in some cases such as Claigeann na Tigh Faire, this difference might be much smaller.

Influence of stoneworks and talus on distribution

Mice trapped in June 1957 showed the effect which walls, cleitean and the storm beach have upon the distribution in the village area. On 8th-9th

June 1957, 32 traps were set in the upper village meadows behind cottages—in a grid well away from stoneworks at point A on the Map, Fig. 1: four lines of eight traps with 10 metre grid squares. Three mice were caught. On the following night, 9th-10th, in similar weather conditions (cold NW winds with showers of rain), 13 mice were caught in 19 traps along the Lady Grange Wall and the storm beach. On the following night, 10th-11th, in similar weather along the walls between the Manse and the Factor's House and on the storm beach, 17 mice were caught in 30 traps. The results can be extended to cover the whole island and to include talus as well as stoneworks. Burrows and runs of field-mice have been noted in the village meadows, in Gleann Mor and on the cliff-terraces well away from stoneworks and talus, but these do not give a true reflection of the size of the population. It would appear that the St. Kilda field-mouse has not a strongly developed burrowing habit, and this may be associated with the shallow soils heavy rainfall, and chances of flooding.

The shelter afforded by stony recesses contributes greatly to the success of the sub-species at St. Kilda. In the building of the several hundred cleitean throughout the island (there are thought to be about 700), man has provided the field-mouse with a widespread refuge from the high winds, rain, and dampness which characterise the climate of St. Kilda. In such blasted situations as the summits of Mullach Sgar, Mullach Mor and Conachair and the saddle at Am Blaid, mice were present in cleitean. It appears highly probable from inspection that such austere ranges would not be colonised in the absence of these structures. Kikkawa (1958) in Fair Isle, found that a locality of short heather was colonised only where a stone dyke provided good shelter. It would be interesting to know if cleitean on the ridges remain tenanted during the winter. Cleitean also provide shelter for a flock of several hundred (about 1000 in summer 1957) Soay sheep. The vegetation, invertebrates in the dry floor raised by the dung and dead of generations of sheep, and the body heat of sheep huddled together in winter, probably all favour the field-mouse.

Influence of altitude on distribution

Height above High Water Mark Ordinary Spring Tides is a direct function of exposure. Exposure, a complex of climatic and topographic variables, can be considered in this case as a basic factor of the eco-system influencing distribution. The influence is modified by the presence of stoneworks and talus. All the samples obtained in the survey of April 1957 were standardised and taken in as many areas as could afford the necessary number of cleitean; they were not chosen because the area looked like yielding a good or a bad catch. The sampling was as random as the cleitean, which appear to be distributed in a fairly random fashion.

Table 2 shows the height above H.W.M.O.S.T. together with numbers of mice and weight of the total catch at each station. Since the numbers caught at each station (maximum possible being 10) left little scope for variation, the weights of the total catch at each station are correlated with the logarithms of the heights above sea-level. The correlation coefficient between weight (y) and $\log_{10}$ height ($\log_{10}$x) is $r=0{\cdot}85$, which is highly significant ($P<0{\cdot}01$).

In his visits to the summits of Mullach Mor and Mullach Sgar by car in winter nights (1957-58), Dr Saundby did not see any mice on the road above 500 feet after October. This might indicate a movement from the high ground in winter. Further unconvincing evidence of a return movement in spring comes from trapping in the Creagan Breac—Lag Aitimir locality: on 19th February 1958, one mouse was caught in 21 traps; on 19th April, four mice in 20 traps; on 20th August 19 mice (8 to 11 adults) in 45 traps. Adult numbers are significantly different between February and August ($\chi^2=5{\cdot}089$), but not between April and August ($\chi^2=1{\cdot}707$). The larger numbers caught in August (about half of which were juvenile) could be explained by reproduction *in situ*. Those of April and August, however, are both higher than that of February and may indicate a spring and summer immigration from the village area.

Influence of the Task Force Operations in 1957 *on distribution*

On 9th-10th June 1957, about seven weeks after the initial landings of the task force, 40 traps were set in the lower meadows at centres of greatest disturbance. Four lines were set as follows:

Line A—10 traps along the west wall of the glebe, between officers' tents and line of kitchen boilers.

Line B—10 traps among pipes, boarding, and in the " workshop " marquee.

Line C—10 traps along the east side of the Lady Grange Wall and in the " equipment " marquee, all above the new road.

Line D—10 traps below the new road on the east side of the Lady Grange Wall, in a wall-cleitan beside the mechanical maintenance bay, at a shore cleitean (beside the beach-head), and in boulders of the storm beach west of the Amhuinn Mhor, beside stone-crushers.

Line A caught three mice; Line B, one; Line C, four; Line D, nine.

On the following night, 10th-11th June, 30 traps were set as follows:

Line E—20 traps between the Manse and Factor's House (beside the church which was used as a cinema and the officers' tents).

Line F—10 traps along the storm beach at the same station as that used in 1955 and 1956 (Boyd, 1956 and above).

Line E caught 12 mice; Line F, five.

Later, on 20th-21st August 1957, 45 traps were set in cleitean immediately surrounding the quarry (Fig. 2) which was opened in the previous June at Creagan Breac; some were placed at Lag Aitimir 100 metres below the quarry, some at Creagan Breac 150 metres above, and a few on both sides of the road at higher levels to the 600 feet contour. In this case 19 mice were caught.

From these results it is clear that the disturbance by the task-force had little immediate effect in displacing the population of field-mice. Line D was placed near the centre of greatest commotion, where a great deal of blasting had taken place and the noise of the stone-crushers and vehicles was loud and continuous over long periods during the day. It was here, however, that the largest catch was obtained. There and elsewhere in the village meadows the catches are similar to what might have been expected (from the catches of 1955 and 1956) had the area remained deserted.

ANALYSIS OF WEIGHTS

The distribution of the population in weight classes of 5 gm. from month to month is shown in Tables 5, 6 and 7. The data of the 1931 survey are not shown because of their less detailed presentation. At all times except in late June 1956, the distribution are unimodal. In December-January, February, March, April, May and early June the population (in the traps) appears completely adult (mice over 25 gm.). In late June the catch is heterogeneous, the juvenile or off-spring peak of the bimodal distribution occurring between 11 and 15 gm., and the adult or parent peak between 36 and 45 gm. In August the catch is also heterogeneous, but, owing to mortality of parents and the influx of maturing off-spring, the off-spring peak dominates the parent peak. It is safe to say that later in the year on the cessation of breeding and the mortality of the parents, the off-spring peak of the year will migrate into the higher weight classes and eclipse the declining parent peak.

The heaviest male so far recorded weighed 56·5 gm., and the heaviest female was 48·5 gm. and was pregnant. The smallest juvenile weighed 7·5 gm. The heaviest males and females of *Apodemus sylvaticus sylvaticus* obtained by Brown (1954) at Silwood Park, Berkshire were both 29 gm. Southern (pers. comm.) has recorded females up to 31 gm. and males up to 32 gm.

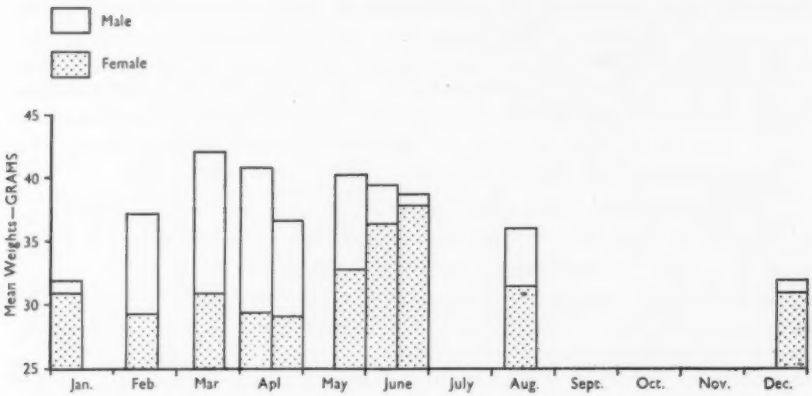

Fig. 3.—Showing the mean weight of males and females at the various times of the year at which measurements have been taken. It should be noted that these measurements are not from the same year; they were taken during the period 1955-58.

in Wytham Woods, Berkshire. The mean weights of adult mice at the various times of the year at which measurements have been taken are shown in Fig. 3. Males are heavier than females though the differences between the sexes varies from month to month. The greatest differences occur in spring and in early autumn when the respective weights were 42·5 gm. male, 30·7 female (March) and 36·0 gm. male, 31·4 female (August). The smallest differences occur in mid-summer and mid-winter. The reason for this variation can be explained

on the basis of the female determining the breeding season, as found by Baker (1930). The males become fecund before the females and rapidly increase in weight due mainly to the growth of the testes (which Baker found were 20 times heavier in summer than in winter) in February and later in June, due to improved food supply. The increase in weight of the females appears to lag behind that of the males by about eight weeks. In July the weight of the fecund males approximates closely to that of the pregnant females, but after pregnancy the weight of the females falls much more rapidly than that of males throughout the autumn.

SEX RATIOS

The sex ratios obtained by a standard method of " Longworth " trapping may not be an accurate measure of the true sex ratio, but the results of such trapping done at different times of the year give an indication of a change in the ratio of adult males to adult females from season to season. Most of the differences which were found in the monthly values, (Table 4) however, could have been obtained by chance. The grand total of adult mice obtained between 1955 and 1958, 183 males to 148 females, is not significantly different from any of the ratios obtained in the various months. The sharp change between early and late June is just insignificant ($\chi^2=3{\cdot}154$). The differences obtained between April, May, early June, August and December-January, February and

TABLE 4

Sex-ratios obtained by trap-surveys done in 1955–58, and others.

Dates	Numbers		Standard Ratio	
	Males	Females	Males	Females
April 1957	60	43	1·4	1
May 1955	18	11	1·6	1
Early June 1957	21	20	1·1	1
Late June 1956	19*	7*	2·7	1
August 1957	28*	26*	1·1	1
Dec.–Jan. 1957–58	10	17	0·6	1
February 1958	27	24	1·1	1
March 1958	25	25	1	1
July–Aug. 1931	?	?	3	1
(Eagle Clarke) 1914	?	?	2	1
(Waterston) 1905	?	?	1	1

* Juveniles (under 25 gm.) excluded.

March are not significant; that between the extreme values 18:11 (May) and 10:17, male : female (December-January) is just not significant ($\chi^2=3{\cdot}527$). The difference between late June and December-January is significant ($\chi^2=6{\cdot}943$), and may be due to the inactivity of nursing females in June, and increased nobility of males.

With the exception of the December-January (1957-58) ratio and a 1:1 obtained by Waterston (1905), males have been recorded slightly in excess of female (Eagle Clarke, 1914; Harrisson & Moy-Thomas 1933; Boyd 1956); 12 males to 10 females seems a close all season estimate obtained by " Longworth " trapping during 1954-58, except for the mid-winter period. Brambell & Hall (1939) obtained a ratio of $50{\cdot}45 \pm 2{\cdot}26$ males per cent in *Microtus agrestis*. Evans (1942) found that the sex ratio of *A. s. sylvaticus* and *Clethrionomys glareolus* varied greatly but approximated to 1:1 in Bagley Wood. Brown (1954) obtained ratios of 42 : 30 and 42 : 42, males : females, in two surveys of *A. s. sylvaticus* in Silwood Park, and in the same surveys 222 : 201 and 266 : 278, males : females in *Microtus agrestis*. Kikkawa (1958) obtained a ratio of 12 : 9 males : females with *A. s. fridariensis* on Fair Isle in May 1956. All are similar to *A. s. hirtensis*.

BREEDING SEASON

The young appear in the traps in the second half of June. Lowe (1957) has shown that *Apodemus* in captivity has a gestation period of 26 days and the young are weaned in 15 days. This timing applied to the St. Kilda field-mouse would probably give first conceptions in late April or early May. Six females and six males were dissected in late April 1958. All the females were perforated but none possessed embryos which could be distinguished with the aid of a hand lens. All of the males had testes partially descended and all had fully grown testes. On 22nd April 1958 two females were obtained with blood filling the vagina which would seem to indicate that they were on the point of parturition or that parturition was just complete. One weighed 43·5 gm. and the other 36 gm. On the same day two other females were found with a milky liquid, like seminal fluid, filling the vagina. These weighed 34·5 and 38·5 gm. and were probably not pregnant. There is, therefore, the possibility that, although most of the young are conceived in about the end of April and appear in the traps about the middle of June, there may be others which are born much earlier; Baker (1930) found pregnancy in Apodemus in April. The number of those early births is probably small, however, since no juvenile mice have been trapped at St. Kilda so far, before mid-June.

The position of the testes may be affected by the environment inside the nest box of the " Longworth " trap and in subsequent handling, and it is in many cases not a convincing indication of whether the individual is fecund. In some cases the testes of males have been seen to descend while under the influence of chloroform. From December to March there is no case of a descent of the testes; in late April all testes are partially or fully descended and remain descended probably until September. The increase in weight observed in males in February and March is probably connected with the maturation of the testes, but no descent appears to take place until April when the females come into breeding condition.

The descent of the testes appears in concert with the perforation of females. In December-January 47 per cent (actual number 8) of the females were perforate, in February 42 (10), and in March 28 (7). The fall off in numbers

of perforate females might be due to the mortality of the older females in the course of the winter. In early April 1958, 43 per cent (6) were perforate and in late April 1958, 94 (16). This last figure is not consistent with that obtained for the same period in 1957 when only 35 per cent (17) were perforate and possibly the breeding season occurs earlier in some years than in others. In June 85 per cent (17) females were found to be perforate and in August this figure had fallen to 15 (4).

The seasonal fluctuations in the proportion of perforate females appearing in the traps shows a decline throughout January-March, a sharp increase in April to a peak between May and July and a decline in August. The period from September to November has not been covered, but during the period the proportion of perforate females increases. This may be due to excessive mortality among juveniles or to a late period of sexual activity in autumn when females of the year are inseminated. Baker (1930) found small autumn peaks in pregnancy in *Apodemus* and also that the numbers of winter pregnancies differed greatly from year to year. In some years there were none. It is probable that the circumstances are somewhat similar at St. Kilda. It may be that females reproduce in the year of birth and there is the possibility of some surviving two winters. Baker and Ransom (1933) studying *Microtus agrestis* in various parts of Britain showed that males become fecund in March, but that pregnancies do not occur till April and May, and the season generally ends in October, though fecund females were present in December in Aberdeenshire.

It is shown by the cumulative evidence of the weight distributions of the separate sexes at intervals throughout the year in Tables 5, 6, 7, coupled with the condition of the testes, vagina, and pregnancy at different times of the year, that the reproduction of the St. Kilda field-mouse is very similar to that of small rodents on the mainland. It is perhaps extraordinary, however, that at St. Kilda some males may be fecund in February when individuals of 45, 48, and 50 gm. were trapped.

[Tables 5, 6, 7 overleaf]

TABLE 5

Distribution of weights in 5 gm. classes of all mice caught.

Date	Grams 0–5	6–10	11–15	16–20	21–25	26–30	31–35	36–40	41–45	46–50	51–55	56–60
17–30th April 1957	—	—	—	—	9	30	31	19	12	2	—	—
24–30th May 1955	—	—	—	—	—	4	4	2	1	—	—	—
7–14th June 1957	—	—	—	—	—	2	12	14	10	3	—	—
22–28th June 1956	—	2	6	4	3	2	7	10	10	2	—	—
5–23rd August 1957	—	—	2	23	80	26	22	24	20	6	2	—
29th Nov. 1957–28th Jan. 1958	—	—	—	—	2	14	7	3	—	1	—	—
7–19th Feb. 1958	—	—	—	—	2	19	13	8	5	4	—	—
11–18th March 1958	—	—	—	—	2	10	10	11	11	5	—	1
3–7th April 1958	—	—	—	—	2	3	10	3	5	3	—	—

TABLE 6

Distribution of weights in 5 gm. classes of males.

Date	Grams											
	0–5	6–10	11–15	16–20	21–25	26–30	31–35	36–40	41–45	46–50	51–55	56–60
17–30th April 1957	—	—	—	—	—	11	17	18	12	2	—	—
24–30th May 1955	—	—	—	—	—	—	3	11	4	3	1	—
7–14th June 1957	—	—	—	—	—	—	4	7	10	1	—	—
22–28th June 1956	—	1	3	3	3	2	5	7	9	1	—	—
5–23rd Aug. 1957	—	—	1	5	23	3	6	8	7	2	2	—
29th Nov. 1957–28th Jan. 1958	—	—	—	—	1	5	2	1	—	1	—	—
7–19th Feb. 1958	—	—	—	—	—	6	6	7	2	6	—	—
11–18th March 1958	—	—	—	—	—	—	1	7	12	4	—	1
3–7th April 1958	—	—	—	—	—	—	1	3	5	3	—	—

TABLE 7

Distribution of weights in 5 gm. classes of females.

Date	Grams 0–5	6–10	11–15	16–20	21–25	26–30	31–35	36–40	41–45	46–50	51–55	56–60
17–30th April 1957	—	—	—	—	9	19	14	1	—	—	—	—
24–30th May 1955	—	—	—	—	—	4	4	2	1	—	—	—
7–14th June 1957	—	—	—	—	—	2	8	7	—	2	—	—
22–28th June 1956	—	2	6	4	3	2	7	10	10	2	—	—
5–23rd Aug. 1957	—	—	1	11	25	9	10	7	—	—	—	—
29th Nov. 1957–28th Jan. 1958	—	—	—	—	1	9	5	2	—	—	—	—
7–19th Feb. 1958	—	—	—	—	2	14	6	2	—	—	—	—
11–18th March 1958	—	—	—	—	2	10	8	5	—	—	—	—
3–7th April 1958	—	—	—	—	2	5	7	—	—	—	—	—

PARASITES

Ectoparasites

The ectoparasites obtained were, fleas: *Ctenophthalinus nobilis vulgaris* Smit, *Nosophyllus fasciatus* Bosc, *Typhloceras poppei* Wagner; mites: not yet identified.

A full account of the fleas is given elsewhere by George (1959).

Out of the 207 mice examined 140 possessed mites and 106 fleas. The average number of fleas obtained from each male was three and female one or 0. Adult males were much more heavily infested than other groups of the population. In 1931 the mites *Laelaps festinus* C. L. Koch and *Enlaelaps stabularis* C. L. Koch were identified. No fleas were recorded then.

Endoparasites

Owing to the strict protection of the field-mouse only nine were killed (some accidentally), and these were dissected. All except one possessed intestinal parasites. Eight had heavy nematode infection. *Rictularia cristata* was the only species obtained, and this has not been previously recorded from mice in Britain. Each mouse had usually three or more nematodes. Three had cestodes, all the specimens being *Hymenolepis diminuta* which has not been recorded from St. Kilda before.

In 1931 no nematodes were recorded, but cestodes were observed though not identified. Waterston (1906) found *Cysticercus fasciolaris* Reed (larva of *Taenia crassicolis* Reed.) but none has been observed in 1957-58. The definitive host of *T. crassicolis* is the domestic cat and the animal is probably now extinct at St. Kilda.

SUMMARY

1. The St. Kilda field-mouse in the village area of Hirta was probably more numerous in 1955 than 1956, but the population in 1955-56 was very much larger than in 1931. The suggestion that the trapping method is sex-selective (Boyd, 1956) is not substantiated.

2. St. Kilda field-mice are present all over Hirta. They are densest in the village area, particularly along the village " street ", and rarest on the ridges.

3. Dry-stoneworks (cleitean, walls, and ruined houses) and talus play a highly significant part in the widespread colonisation of Hirta. There is a suggestion that the community on the higher levels (above 500 feet) may move to the lower ground during the winter, and return in the spring. The association of sheep with cleitean may play an important role in the ecology of the field-mouse at the present time.

4. Altitude (being a function of exposure to weather) plays a highly significant role in the distribution of the field-mouse; the value of r for total weight obtained by a standard sample and the logarithm of the height above sea-level is 0·85.

5. The incursion of the Royal Air Force task force into the island has not so far displaced or depleted the field-mouse population. Mice were numerous at centres of greatest human activity.

6. Mice are heaviest in May and June and lightest in December and January. The mean weight of adult males varies from 31·8 gm. to 40·2, and that of adult females from 29·4 gm. to 37·8. The heaviest male was 54·2 gm. and heaviest female 48·5. The lightest juvenile was 7·5 gm. The greatest differences between the mean weights of the sexes occur in February (7·8 gm.) and August (4·6 gm.), and smallest in December-January (1 gm.) and late June (0·9 gm.).

7. The grand total sex-ratio from "Longworth" trapping from 1955 to 1958 is 183 males and 148 females. None of the separate sex ratios obtained in the monthly surveys were significantly different from the grand total ratio.

8. Males become fecund in February and March. Females become pregnant from April to June. First young appear in the traps in late June (first born in late May or early June), and females probably become quiescent before males. Some perforate females occur in spring before males become active and these may reproduce in the year of birth. On the other hand some females may survive two winters.

10. The fleas found on the St. Kilda field-mouse were *Ctenophthalinus nobilis* Smit, *Nosophyllus fusciatus* Bose and the mites *Typhloceras poppei* Wagner. The nematode *Rictularia cristata* Froclich 1802 and the cestode *Hymenolepis diminuta* Reed 1819 were obtained from the intestines of the mice.

ACKNOWLEDGMENTS

The author wishes to thank Mr K. Williamson, Dr R. P. Saundby and Mr J. T. D. Wilson for their services at St. Kilda. Mr Williamson, Dr J. D. Lockie, Dr W. J. Eggeling and Mr H. N. Southern kindly read the manuscript and gave helpful criticism. The fleas were identified by Mr R. S. George, the nematode by Mr W. G. Ingles and the cestode by Mr S. Prudhoe. Statistical advice was given by Dr R. A. Robb. The visit in 1956 was made with the permission of the late Marquis of Bute, and a grant was given then by the University Court of the University of Glasgow. The figures were drawn by Mrs E. L. Bradshaw.

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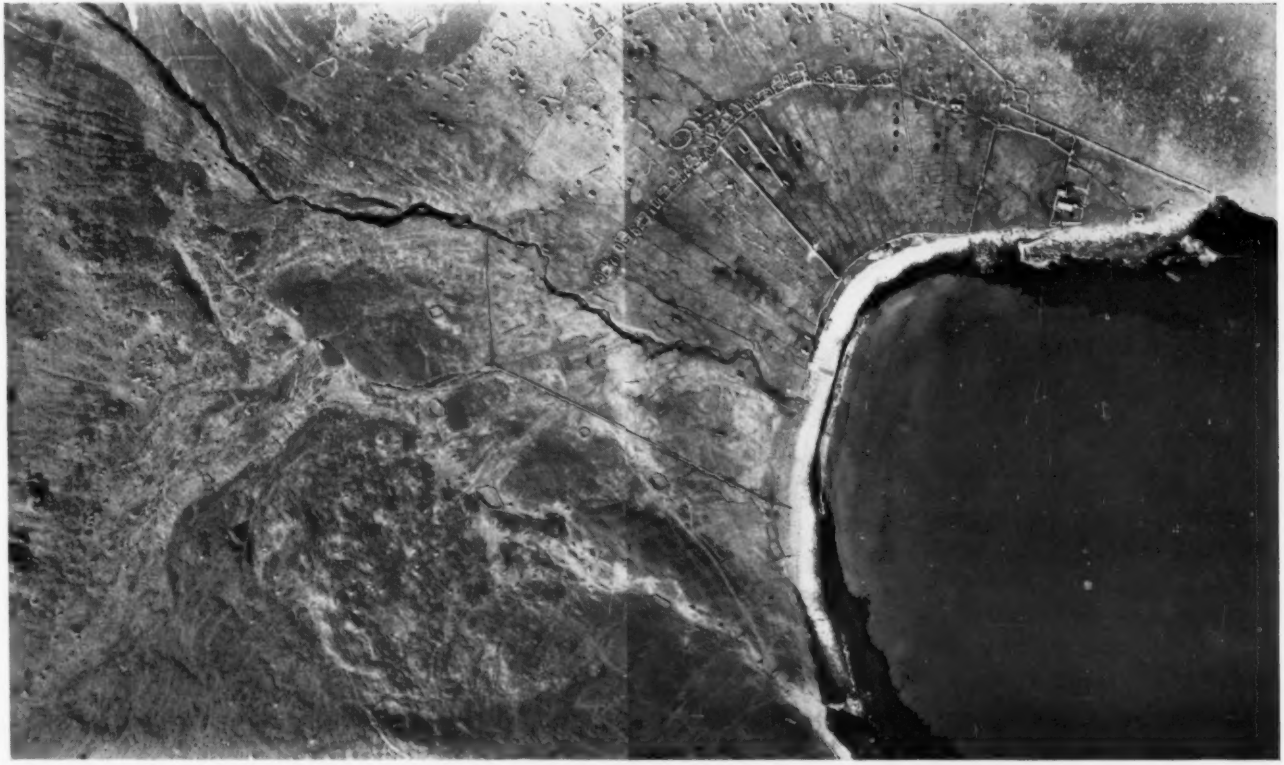

Aerial view of the village area of St. Kilda showing the roofless cottages, the derelict meadows, the walls and *cleatean*. The manse and church are at the extreme right of the picture. *Cleatean* (Dry-stone cells) can be seen scattered on the slopes to the top and left of the picture.

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THE PHOTOSENSITIVITY OF THE SEA URCHIN *DIADEMA ANTILLARUM* PHILIPPI: RESPONSES TO INCREASES IN LIGHT INTENSITY

BY

N. MILLOTT AND M. YOSHIDA

Department of Zoology, Bedford College, University of London

[Accepted 14th October 1958]

(With 1 plate and 1 figure in the text)

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INTRODUCTION

Diadema responds to changes in light intensity by spine movements. The spines respond both to increases and decreases in light intensity by single jerks, or by continued waving which may be prolonged. The responses were examined originally by von Uexküll (1900) and more recently, responses to shadows have been examined by Millott (1954) and Millott & Yoshida (1957). The responses to shadows proved to be reflexes involving the radial nerves; the receptive surface is diffuse, the entire skin being sensitive as well as the radial nerves. (Yoshida & Millott, 1959).

Responses to increases in intensity have been examined only by von Uexküll, who maintained that they differ from responses to shadows in their nerve pathways; the mechanism for responses to increases occurring wholly outside the test and not involving the radial nerves.

Such a different anatomical basis for reactions to changes in intensity which differ merely in sign, needs re-examination in the light of our more recent studies.

METHODS

Experiments were conducted in a dark room lighted by an overhead "Safelight", using apparatus essentially similar to that already described (Millott & Yoshida, 1957). The internal or external surface of a piece of test was stimulated from above, by a light beam concentrated by various lens systems to illuminate small areas. The spines projected upwards or were allowed to hang downwards, in another light beam, so as to produce a sharp

shadow on a ground glass screen. Their movement was observed on this, and from above. It was recorded by an oscilloscope camera focused on the screen.

ANALYSIS OF THE SPINE RESPONSE

Responses to changes in intensity are shown by the spines of isolated pieces of body wall. Responses to intensity increase resemble in many respects those which follow decreases (Pl. 1, A and B, figs. 1, 4, 5 and 6), though the threshold intensity is about one thousand times greater.

Participation of the nervous system is indicated by the widespread response which results when a narrow light beam is projected on to any part of the radial nerve, by the rapid spread of the response following localised stimulation, and particularly clearly by the necessity for the radial nerve. If this be removed, the response is abolished (Pl. 1, fig. 2). This is not merely an indirect effect on the spine muscles of cutting some of their nerves, for they still respond vigorously to electrical stimulation, after removal of the radial nerve (Pl. 1, fig. 3).

Obviously no centre in the oral nerve ring is directly involved, and the nerve pathways pass through the radial nerve. It remains to be shown whether the reaction involves elements widely distributed in the radial nerve or whether some special part of it is concerned.

If the radial nerve is cut across in the region of the ambitus, after allowing some 20 minutes for recovery, a light beam projected on to both sides of the cut elicits a clear response in the spines on either side (Pl. 1, fig. 4A), but if the cut is widened so that a length of the nerve corresponding to a linear series of about eight ampullae is removed, the spines immediately beneath the denervated area fail to respond, while those on either side of the cut respond vigorously (Pl. 1, fig. 5A).

A complementary experiment may be performed in which both oral and aboral regions of the radial nerve are removed, leaving the ambital region intact. When the internal surface of such a preparation is stimulated by a light beam, only the spines below the intact region of the nerve respond to light. This means that to obtain a response from a given group of spines, the portion of the radial nerve which underlies them is essential.

There is thus no main centre in the radial nerve and the response appears to be a localised reflex which conforms with indications of a diffuse receptive surface reported below.

The restriction of the response to regions in which the radial nerve was intact is puzzling in the light of the demonstration of a conducting system in echinoids by Kinoshita (1941), involving chain reflexes limited to the skin, whereby excitation could spread from spine to spine. Occasionally, however, a very few spines in denervated areas moved, usually very slowly, after a long delay (Pl. 1, fig. 6A). This type of response differs markedly in appearance from that which first follows illumination, suggesting that impulses may have reached the spines by an indirect route such as that which Kinoshita described.

THE PHOTORECEPTIVE SURFACE

Sensitivity to light in various areas was tested by simple experiments.

A light beam directed on to the spines, unlike a similar beam directed on to the test, elicits no response (Pl. 1, fig. 7).

In determining the relative sensitivity of various regions of the outside surface, preparations were allowed to adapt in dim light for at least 20 minutes and then small areas were briefly illuminated at five minute intervals.

An unavoidable difficulty in this type of experiment stems from the spiny and irregular character of the echinoid surface. Though small light spots are obviously desirable, their use produced misleading results because the shafts of the spines in altering their stance during an experiment, obstructed the very narrow light beam used. If the spines were cut short, even in limited areas, the responses became markedly erratic, presumably owing to the disturbances which result. Using a glass rod drawn to a fine point as a light conductor, with its tip close against the skin over the test, also proved unsatisfactory, because the light intensity that could be attained this way, proved insufficient to elicit a response to lighting, though more than adequate to produce a response when the light was cut off. To produce consistent responses, and to minimise the interfering effect of the spines, it was necessary to compromise by illuminating larger areas. For these experiments, the most satisfactory illumination was a focused beam from a standard microscope point light lamp producing a spot about 0·5 cm. in diameter.

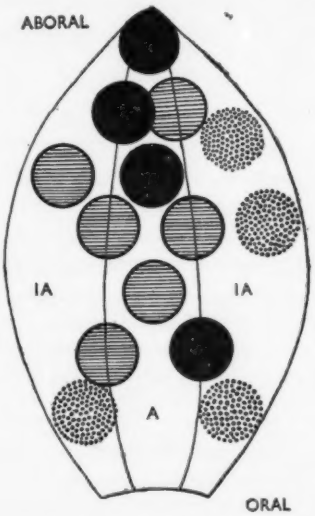

Fig. 1.—Map made from scanning experiments (p. 69) showing the distribution of sensitivity on the outside surface of an isolated piece of body wall. Black areas are most sensitive; stippled, least sensitive, horizontally shaded are intermediate. Areas are drawn approximately to scale. A. Ambulacral area. I.A. Inter-ambulacral area.

The results of scanning the surface in this way are shown in Fig. 1. All the outside surface proved sensitive, but using the relative size of the response

as a rough index, they are not equally so. Thus in general, more vigorous and prolonged responses resulted from stimulating the ambulacral areas than from stimulating the inter-ambulacral.

These findings confirm earlier ones where scanning with a smaller spot from a less powerful lamp, revealed sensitivity only in the ambulacral areas.

DISCUSSION

These results recall those previously obtained when responses to decreases in intensity were studied (Millott, 1954).

The photosensitive areas in both cases proved diffuse, extending over the outer surface of the body wall, and internally, along the ambulacra. The most sensitive areas of the skin occur in the ambulacra. Structures corresponding to morphologically defined photoreceptors have yet to be found.

Again, as in the shadow response, it is noteworthy that the distribution of the photosensitive areas corresponds with that of the main nervous areas, namely the superficial nerve layer and the radial nerves. Such correspondence conforms with our recent findings (Yoshida & Millott, 1959), which provide stronger evidence that receptive elements exist in the nervous system.

The importance of the radial nerve in responses to increases in intensity, as well as to decreases, invalidates a sharp distinction made by von Uexküll between the nerve pathways involved in the two kinds of response and opens the way for making further comparison between them, based on future work, especially in relation to what is known of " on " and " off " effects in retinae.

ACKNOWLEDGMENTS

We are greatly indebted to the Zoological Society of London, and especially to Dr H. G. Vevers, for much help. Similar thanks are also due to the Medical Research Council for financial support.

SUMMARY

Diadema responds to increases in light intensity by spine movements, which contrary to the statements of von Uexküll, are reflexes involving the radial nerve. The receptive surface is diffuse extending over the skin, the most sensitive areas being associated with the radial nerve.

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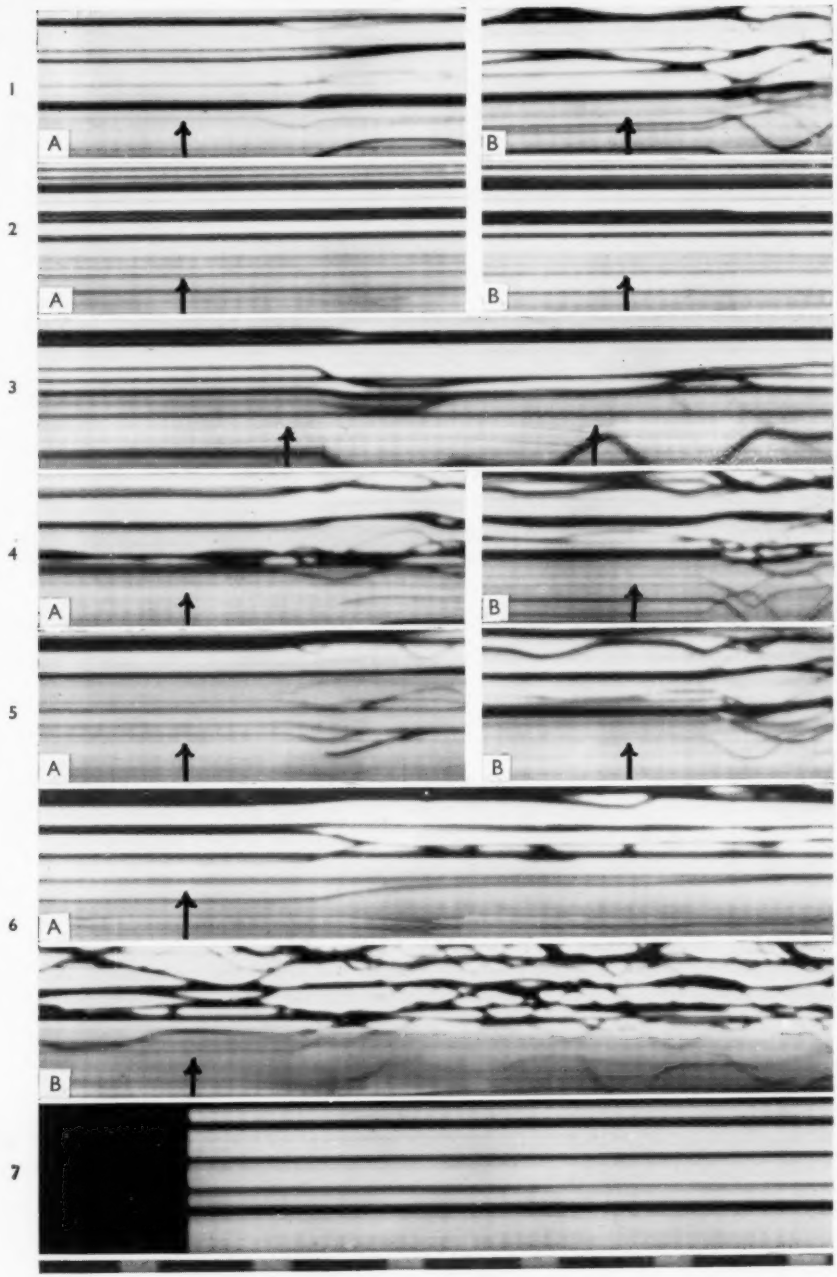

The photosensitivity of *Diadema antillarum*.

EXPLANATION OF THE PLATE

Photographic records of spine movements (see p. 68). The time scale for all records is at the bottom, one white and one adjacent black area, marking intervals of one second. Each record should be read from left to right.

Fig. 1.—Typical response of an isolated piece of test. A. Light admitted at arrow. B. Light extinguished at arrow.

Fig. 2.—Effect of removing the radial nerve of the same preparation. A. Light admitted at arrow. B. Light extinguished at arrow.

Fig. 3.—Effect of stimulating electrically the outer surface of the foregoing preparation. The stimulus was continued between the two arrows.

Fig. 4.—Transection of the radial nerve; the effect of a simple cut. The preparation was arranged so that spines situated above the intact regions of the radial nerve on either side of the cut, were included in the photograph. A. Light admitted at arrow. B. Light extinguished at arrow.

Fig. 5.—The effect of widening the cut made previously. The spines in the centre, which remain stationary, correspond to the area from which the radial nerve had been removed. A. Light admitted at arrow. B. Light extinguished at arrow.

Fig. 6.—The effect of removing the entire radial nerve on one side of the cut. The preparation was arranged so that the spines in the lower half of the photograph were in the denervated area. Note the relatively slow and delayed response of some of the spines (see p. 68). A. Light admitted at arrow. B. Light extinguished at arrow.

Fig. 7.—The insensitivity of the surface of the spine shaft. Light admitted to the spines (end of black area) elicits no response.

THE NASAL FOSSA OF A FOETAL GORILLA

BY

A. J. E. CAVE, M.D., D.Sc., F.Z.S.

St. Bartholomew's Hospital Medical College, University of London

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(With 2 figures in the text)

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INTRODUCTION

The need was indicated by Cave & Haines (1940) for the study of additional specimens of the anthropoid ape nasal fossa, especially in the wet (mucosal) state, towards augmentation of the still scanty knowledge available concerning this particular morphological field, which, apart from its intrinsic interest, is not without significance in the elucidation of problems of taxonomy and phylogeny.

Those authors detailed the nasal fossa anatomy of six very young post-natal gorilla specimens (three mucosal, three macerated) but were without prenatal material ; no earlier study of foetal material was available in the literature and none appears to have been published in the interim. Hence no apology is necessary for the submission of the present account, describing, for the first time, the condition of parts in the nasal fossa of a gorilla foetus.

MATERIAL

The specimen (R.223, author's collection) described herein is a spirit-preserved male animal, whose precise foetal age is unknown but whose size, general proportions and external morphology indicate its being not far from full term. Its sitting height (crown–rump length) is some 240 mm., which may be compared with the corresponding measurement of 275 mm. recorded for a neo-natal female gorilla born in captivity at Columbus, Ohio. (The heart and thoracic viscera of the present specimen have been figured and briefly described by Franklin (1948)).

The right nasal fossa is depicted in the undissected state in Fig. 1 and in the dissected state in Fig. 2.

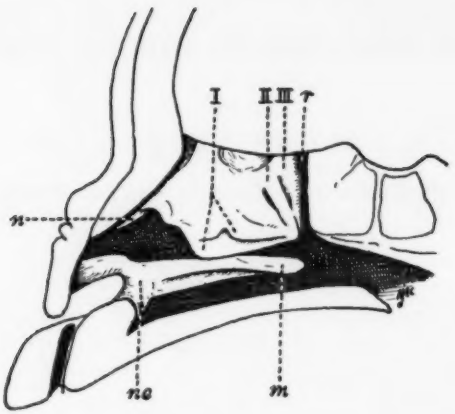

Fig. 1.—Right nasal fossa of foetal gorilla (R.223), undissected.
m=maxilloturbinal ; n=nasoturbinal ; n.e.=narial eminence ; r=recessus presphenoidalis ; I, II, III=ethmoturbinals.

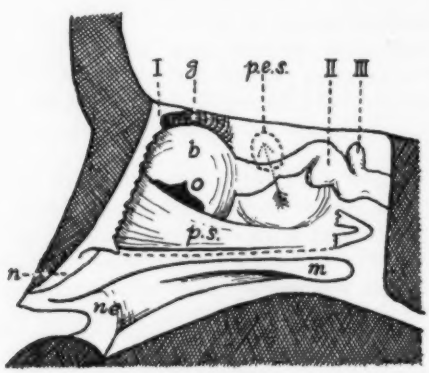

Fig. 2.—Right nasal fossa of foetal gorilla (R. 223), dissected by removal of the greater part of ethmoturbinal I. (Semi-diagrammatic).
b=bulla ethmoidalis ; g=suprabullar groove ; m=maxilloturbinal ; n=nasoturbinal ; n.e.=narial eminence ; o=ostium maxillare ; p.e.s.=posterior ethmoidal sinus (ostium) ; p.s.=plica semilunaris ; I, II, III=ethmoturbinals.

The presphenoid and postsphenoid remain still discrete : the former is as yet incompletely ossified, the latter is ossified in its anterior moiety only. The basioccipital is well, but not entirely, ossified.

ANATOMY

On inspection the nasal fossa gives the impression of being supero-inferiorly compressed with extremely narrow meatuses and closely-packed turbinals, but the condition of parts is nowise essentially different from that observed in very young post-natal specimens (Cave & Haines, 1940). A maxillo-turbinal, continuous anteriorly with a well-marked intra-narial eminence, extends backwards the length of the lateral fossa wall to terminate close to the anterior aspect of the presphenoid : it is somewhat folded upon itself, with a resultant groove or overlap upon its septal aspect. A well-marked curved ridge below and immediately adjacent to the naso-frontal region represents a naso-turbinal, of the typically reduced primate type. Continuous with the naso-turbinal is an ethmoturbinal I, showing some degree of plication and extending almost the whole length of the lateral wall of the nasal fossa. Its anterior and convex portion is attached superiorly to the nasal fossa roof and behind this attachment a distinct depression is visible : its angled, inferior free margin partially overlaps the maxillo-turbinal, close to whose posterior end it terminates in a double " root ", separated by but a narrow chink from ethmo-turbinal II. This last is a narrow, oval, restricted and almost vertical elevation on the lateral fossa wall, separated infero-anteriorly by a cleft-like superior meatus from ethmoturbinal I and separated supero-posteriorly by a faint linear depression from a minor posterior elevation which represents an ill-developed ethmoturbinal III, continuous posteriorly with the sphenoidal region. In the undisturbed condition of the parts the inferior meatus is visible throughout its entire extent, and receives the naso-lacrimal duct, or bulla, whose precise degree of dilatation remains unascertained. The middle meatus presents chiefly its most anterior portion ; the superior meatus appears as nothing more than an almost linear cleft between ethmoturbinals I and II ; the supreme meatus, between ethmoturbinals II and III, is a mere mucosal furrow. The ethmoturbinal posterior extremities are closely contiguous to the anterior aspect of the presphenoid, a deep, vertical and narrow recess alone intervening.

Removal of ethmoturbinal I reveals the full extent of the lateral wall of the nasal fossa and of the middle and inferior meatuses. The following structures are immediately recognisable—a bulla ethmoidalis, a suprabullar groove, a sulcus semilunaris, a plica semilunaris, an ostium maxillare, the superior crus of ethmoturbinal II and the rudimentary ethmoturbinal III. Of these the bulla, the plica and the ostium maxillare are the most obtrusive.

The bulla ethmoidalis is a relatively large, rounded and prominent elevation in the forepart of the lateral nasal fossa wall, lying normally under cover of the convex anterior portion of ethmoturbinal I. About the size and shape of a pea, it overhangs the ostium maxillare. Posteriorly it is continuous with a low but distinct ridge which connects the bullar region to ethmoturbinal II and which represents the superior crus of that turbinal.

Above the bulla lies a blind, curvilinear depression (suprabullar groove) devoid of any outpouchings or expansions, so that neither a frontal sinus nor an anterior ethmoidal sinus is as yet in process of development.

Immediately below the bulla a narrow mucosal gutter (sulcus semilunaris) is bounded inferiorly by a strongly-developed, semicrescentic plica semilunaris. An ovally elongate orifice (ostium maxillare) opens into the sulcus semilunaris between the bulla and the plica, and so directly into the middle meatus. The superior ostial margin is thick, rounded and somewhat lip-like. Through the ostium the introduced probe enters immediately a well-established maxillary sinus.

The sulcus semilunaris is narrow : it extends consecutively anterior, inferior and slightly posterior to the bulla ethmoidalis.

The plica semilunaris is an extremely prominent mucosal ridge which conceals the underlying ethmoidal processus uncinatus. Deep and thick anteriorly it tapers gradually in a posterior direction to fade into the lateral wall of the nasal fossa about the level of attachment of the " root " of ethmoturbinal I. It is closely apposed throughout to the bullar region and its relatively large size suggests a substantial development of the uncinate process (a structure subject to great variation in its degree of manifestation in gorilla crania).

The infra-plical portion of the middle meatal wall is featureless. The superior meatus is limited above by the above-mentioned low ridge (superior crus) connecting the main portion (inferior crus) of ethmoturbinal II to the bullar region. The meatal floor between this ridge and the posterior end of the plica semilunaris is distinctly convex and suggestive of sinus formation. About the junction of the constituent crura of ethmoturbinal II the mucosal flooring of the meatus exhibits a small dimple, the mouth of a mucosal sac, which admits the passage of a fine probe underneath the inferior free edge of the superior crus towards a rounded orifice lying thereabove. This orifice is the mouth of a well-established posterior ethmoidal air cell. After removal of the mucosa from the hinder part of the nasal fossa wall the entrance to this sinus becomes more clearly apparent, although its ostium remains hidden by the superior crus of ethmoturbinal II. The rudimentary ethmoturbinal III is likewise then plainly apparent as a free, oval projection, imperfectly separated from the mass of ethmoturbinal II by a faint intervening groove.

The presphenoid is everywhere solid and without indication of even incipient pneumatisation.

Thus, in specimen R.223, of undeterminable but obviously advanced prenatal development, the only paranasal sinuses established are the maxillary and a single posterior ethmoidal : there is not the least suggestion of the commencement of other sinuses. This evidence confirms the inference derived from examination of very young post-natal gorilla specimens (Cave & Haines, 1940) regarding the sequence of development of the paranasal sinuses in *Gorilla*. The full complement of gorilla sinuses comprises a maxillary, a sphenoidal, a frontal and a maximum of three (one anterior, two posterior) ethmoidal sinuses. (The maxillary sinus is probably the sole member of the series homologous with its nominal counterpart in non-primate forms. The sphenoidal sinus is certainly not homologous with the similarly designated, but morphologically wholly different, sub-primate cavity, while ethmoidal sinuses

are neomorphs confined to *Gorilla*, *Pan* and *Homo* : the frontal sinus in these forms is essentially an "isolated" ethmoidal cell, arising, in *Gorilla* and sometimes in *Homo*, from the suprabullar groove).

In *Gorilla* the maxillary sinus is the first paranasal air cavity to appear ontogenetically and is followed by the two posterior ethmoidal sinuses, the hindermost cell preceding the foremost. The sequence of subsequent sinus formation remains uncertain for want of appropriate study material : but it would seem from examination of young post-natal specimens that sphenoidal pneumatisation proceeds more or less *pari passu* with the more tardy development of the frontal sinus and its concomitant anterior ethmoidal sinus.

The fronto-ethmoidal sinus complex in *Gorilla*, fully established by the time the milk dentition is acquired, remains in its entirety up to early adult life. Thereafter, however, the ethmoidal cells, ontogenetically so precocious, suffer a progressive obliteration through the sustained expansion of the more dominant frontal and maxillary sinuses. In skulls of old animals, therefore, either no trace whatsoever remains of ethmoidal cells or the hindermost only of the two posterior ethmoidal cells persists, on one or on both sides. This retrogression of ethmoidal sinuses, so characteristic of *Gorilla*, contrasts strongly with conditions in *Homo*, wherein a profusion of ethmoidal cells maintains a steady topographical expansion throughout life.

SUMMARY

1. The anatomy of the nasal fossa is described for a gorilla foetus approaching term.

2. Of the paranasal sinuses, a maxillary and a posterior ethmoidal sinus alone are present and are well established.

3. Sphenoidal, frontal and anterior ethmoidal sinuses have not as yet begun to develop.

4. Beneath a prominent bulla ethmoidalis and above a strongly developed plica semilunaris, an ostium maxillare opens directly into the middle meatus.

5. In addition to a naso-turbinal, a maxillo-turbinal and ethmoturbinals I and II, a rudimentary ethmoturbinal III is present.

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THE SYSTEMATIC AND ADAPTIVE SIGNIFICANCE OF THE VIBRISSAE IN THE MARSUPIALIA*

BY

A. G. LYNE, B.Sc., PH.D., F.Z.S.

Zoological Laboratory, University of Cambridge and Department of Zoology, University of Tasmania†

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(With 5 plates and 26 figures in the text)

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INTRODUCTION

The possession of a hairy coat distinguishes the mammals from other classes of vertebrates. It is understandable that a character so distinctive and of such systematic importance should have been included among features of taxonomic value in the classification of mammals ; but it is somewhat surprising that for the most part attention has been paid to the coat in relation to general texture, colour and colour pattern only, and not to any detailed analysis of

* Part of a thesis approved by the University of Tasmania for the award of the Ph.D. Degree.

† Present address : Division of Animal Health and Production, C.S.I.R.O., Sheep Biology Laboratory, Prospect, N.S.W., Australia.

the hair types and structure. The taxonomic features which have received most attention provide the major, sometimes the sole, basis of distinction between certain species of subspecies.

Vibrissae, or sinus hairs, are found in limited special areas of most mammals and are often referred to as tactile hairs, as distinct from the pelage hairs which cover the general body surface. Ontogenetically, vibrissae are usually the first hairs to appear and are often the largest hairs of all : they arise from deep-seated and specialized follicles. Some, such as those on the upper lip of the rat, establish connections with the subjacent striated musculature and are under voluntary control ; others are not under such control.

References to the development of mammalian vibrissae are scanty. Szymonowicz (1936) made a comparative examination of the innervation of the vibrissae, and Vincent (1913) studied the innervation, anatomy and function of the tactile hair of the white rat. Hardy (1951) and Davidson & Hardy (1952) investigated *in vitro* the development of mouse vibrissa-follicles and small keratinized hairs.

Between the fur-hairs at one extreme and the tactile vibrissae at the other, appears a rather wide gap, both in size and structure, but a complete series of intermediate forms is to be found in many species. Toldt (1910) has carefully investigated this transition between fur and bristles. Botezat (1897) made similar studies, particularly of the nerve supply to the follicles, of hairs ranging from bristles to the most highly specialized tactile vibrissae. Danforth (1925) also claimed that, since there exists a continuous series between pelage hair-follicles and vibrissa-follicles, the two kinds of hairs were homologous, and that their differences were due to different organogenetic influences. Hardy (1951) and Davidson & Hardy (1952) claim, however, that the follicles of vibrissae and of pelage hairs in the mouse differ in many of their histological features and that these differences are maintained in tissue culture. Melaragno & Montagna (1953) also describe structural differences between the follicles of vibrissae and those of pelage hairs in the mouse. In the marsupials the similarities or differences which exist between vibrissa and pelage hair follicles have not been examined.

The vibrissae of any individual mammal are few in number and their distribution is limited for the most part to the lips, cheek, supraorbital region, and wrist. Less commonly they occur on the lateral aspect of the forearm and near the heel.

A preliminary examination of the distribution of the vibrissae in several Australian bandicoots (Lyne, 1951, 1952) suggested that these structures would prove of considerable taxonomic value in marsupials. Earlier, both Beddard (1900, 1902) and Pocock (1914) directed attention to the possible systematic importance of the vibrissae in various species. Beddard (1902) examined the forearms of a large number of mammals and invariably found vibrissae near the wrist in those species which use their fore-limbs as climbing or grasping organs, or both. He found, however, that when the fore-limbs are purely ambulatory, ulnar carpal vibrissae are absent. Pocock (1914) established certain general principles as to the constancy of groups of facial vibrissae in a large series of mammals. He found that within each order, the

species which have fewer groups of vibrissae are the more specialized types, whereas those retaining all or most groups are the more generalized types. He concluded that a full set of vibrissae was to be considered a primitive characteristic. Pocock's studies also suggested that the distribution of the facial vibrissae is directly related to the mode of life of the species. For example, the vibrissae are absent or greatly reduced in the monotreme, marsupial and edentate ant-eaters, and they are highly developed in many active arboreal mammals.

Neither Beddard nor Pocock made any attempt to count the actual number of vibrissae present in the various situations. Danforth (1925), however, working chiefly on the mouse, found the number of vibrissae in each group to be remarkably constant within a species. Wood Jones (1920, 1921, 1922a, 1922b, 1923a, 1923b, 1923c, 1923d, 1924a, 1924b, 1924c) described the distribution of the vibrissae in a number of Australian marsupials and Boardman (1943, 1945) gave descriptions of the vibrissae in several other marsupial species.

In view of the unique zoological position occupied by the marsupials and the comparative rarity of many species, it was considered desirable to make a more general survey of the frequency and distribution of the vibrissae of the marsupial head and limbs. The present paper deals especially with the distribution of vibrissae in representatives of all the families of marsupials. A total of 528 specimens from fifty-four species has been examined. Nine species are from South America, and the forty-five species from Australasia include nineteen of the twenty living species recorded from Tasmania. In several species, particularly *Pseudocheirus convolutor* and *Trichosurus vulpecula*, the distribution of the vibrissae is noted only in the larger pouch-young bearing the full adult complement of vibrissae. These two species have been examined especially to discover any possible sex differences in the number and arrangement of vibrissae.

This investigation has also sought to ascertain whether the distribution of the vibrissae in the marsupials throws any light on the relationships of the major divisions of the group and upon the affinities of the group as a whole.

The taxonomic nomenclature used for the Australian material in general follows that of Iredale and Troughton's check list (1934).

GENERAL DISTRIBUTION OF THE VIBRISSAE

The distribution of the principal groups of vibrissae in marsupials is shown in Fig. 1.

With the exception of the interramal set, the vibrissae are all in paired groups, and according to their position on the head and limbs, they may be referred to the following categories :

1. *Mystacial.* The well-known " whiskers " on the muzzle and upper lip. The vibrissae of this group are usually arranged in well defined longitudinal rows.
2. *Genal.* One or two groups or isolated vibrissae on the cheek over the malar bone. In the marsupials the genal set is nearly always single and it is usually situated below the posterior (lateral) canthus.

3. *Supraorbital.* The set above the eye, generally above its anterior (medial) portion, but occasionally further back.
4. *Interramal.* An unpaired group of one or more vibrissae on the mid ventral line behind the chin, generally at about the level of a line joining the angles of the mouth.
5. *Submental.* Vibrissae on the chin and lower lip. Often there are two well defined longitudinal rows, one on either side of the chin, in addition to smaller ones less regularly arranged.
6. *Suborbital.* Vibrissae beneath the eye, present mainly in large herbivores including some of the wallabies and kangaroos.
7. *Rhinal.* Vibrissae on either side of the dorsum of the muzzle, immediately behind the rhinarium.
8. *Ulnar carpal.* A set of one or more vibrissae on the volar surface of the forearm near the wrist.
9. *Medial antebrachial.* Vibrissae usually situated about half-way along the postaxial margin of the forearm, sometimes at the level of the ulnar carpal papilla.
10. *Anconeal.* Vibrissae on or near the elbow but sometimes situated near the middle of the forearm.
11. *Calcaneal.* Vibrissae situated on the inner side of the ankle.

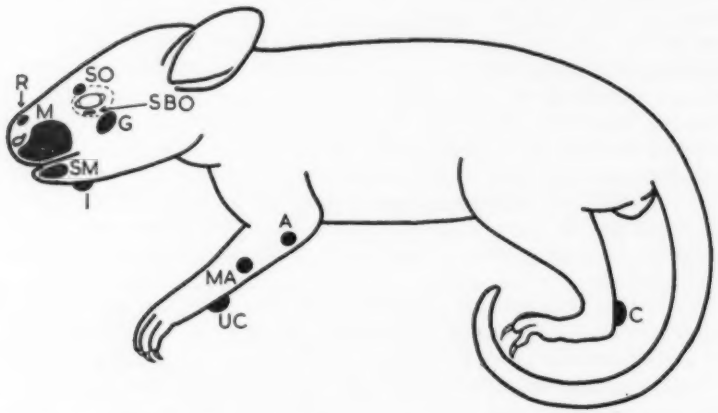


Fig. 1.—Diagrammatic representation of a marsupial to show the distribution of the principal groups of vibrissae. A, anconeal ; C, calcaneal ; G, genal ; I, interramal ; M, mystacial ; MA, medial antebrachial ; R, rhinal ; SBO, suborbital ; SM, submental ; SO, supraorbital ; UC, ulnar carpal.

MATERIAL, METHODS AND ABBREVIATIONS

1. *Material and methods*

The material has been obtained from a number of sources. Approximately half the Tasmanian animals examined were collected by the author during 1949–50 and during 1952–53. The remainder of the Tasmanian material was lent by the Tasmanian Museum, Hobart, and the National Museum of Victoria, Melbourne.

Material in the National Museum of Victoria was examined (1950, 1953) and in the British Museum (Natural History), London, and in the University Museum of Zoology, Cambridge (1951–53). The late Professor J. P. Hill kindly permitted examination of specimens in the Embryology Department, University College, London. The Zoological Society of London kindly made available a number of specimens in their Prosectorium. Mr G. B. Sharman, Department of Zoology, University of Western Australia, provided specimens of two West Australian marsupials.

The greater part of this investigation has been carried out on pouch-young preserved in spirit. Unfortunately, juvenile material of a number of species was not readily available and it was necessary, therefore, to examine adult specimens. In several cases both juvenile and adult material of the one species has been examined.

Most of the Tasmanian pouch-young procured personally were taken from freshly-caught animals. Nearly all of these pouch-young were fixed in Bouin's fluid in the field and stored in 70–80 per cent alcohol. Most of the adult specimens were preserved in 5 per cent formalin.

As there are no records of age, the head-plus-body length (i.e. tip of snout to base of tail mid-dorsally) of most specimens is noted (in millimetres). Preserved body weights and length measurements of head, tail, external ear, pes and manus have been recorded for many specimens, but are not included here.

All observations on the number and arrangement of vibrissae have been made with the aid of a low-power binocular microscope.

2. *Abbreviations*

H+B,	—Head and body length in millimetres.
L,	—Left side.
R,	—Right side.
B. M.,	—British Museum (Natural History), London.
Nat. Mus. Vict.,	—National Museum of Victoria, Melbourne.
Tas. Mus.,	—Tasmanian Museum, Hobart.
Univ. Mus. Zool. Camb.,	—University Museum of Zoology, Cambridge.
Zool. Soc. Lond.,	—Zoological Society of London.

Registration numbers prefixed with the letter " A " refer to specimens in the University Museum of Zoology, Cambridge, England.

Registration numbers prefixed with letters " C ", " M ", or " R " (except where otherwise indicated) refer to specimens in the National Museum of Victoria, Melbourne.

Registration numbers not prefixed with a letter (except where otherwise indicated) refer to specimens in the Tasmanian Museum, Hobart.

Registration numbers prefixed with the letter " X " refer to specimens from the author's collection.

DESCRIPTION OF MATERIAL

Suborder POLYPROTODONTIA

Family I. **Didelphidae** (Pl. 1,A and Figs. 2–3)

Material

1. *Didelphis marsupialis* Linnaeus var. Common American opossum.

(a) A4. 9/14 and 15—two juvenile litter mates ; male (H+B 123) and female (H+B 125) ; Marajo Isle, Brazil. (b) Litter of seven pouch-young (H+B 103) ; three males and four females from Rio de Janeiro. Embryology Department, University College, London (Professor J. P. Hill collection).

2. *Didelphis marsupialis* var. *azarae* Temminck. Azara's opossum.

B.M. 97.11.7. 83–84—two specimens, probably litter mates ; male (H+B 155) and female (H+B 150) ; Cayambé, Ecuador.

3. *Metachirus opossum* (Linnaeus). Quica opossum. A4. 11/3—juvenile male (H+B 140) ; Merida, Venezuela.

4. *Marmosa cinerea* Temminck. Ashy opossum. A4. 21/2, 5 and 6—two males and one female ; A4. 21/2 female (H+B 200), A4. 21/5 male (H+B 158) and A4. 21/6 male (H+B 67) ; Merida, Venezuela.

5. *Marmosa murina* Linnaeus. Murine opossum. B.M. 95.4.27.6—female (H+B 110) ; Managua, Nicaragua.

6. *Dromiciops australis* (Phillipi). Chiloé Island opossum. Zool. Soc. Lond. M45–female (H+B 110) ; Chiloé Island, Chile.

7. *Peramys dimidiatus* Wagner. Yellow-sided opossum. B.M. 0.6.29.16—female (H+B 138) ; Palmeira, Parana, Brazil.

8. *Chironectes minimus* (Zimmermann). Water opossum. Two females. (a) B.M. 94.8.6.15 (H+B 115) ; Chanchamayo, Perú. (b) B.M. 88.11.30.16 (H+B 170) ; San Lorenzo, Rio Grande do Sul, Brazil.

A summary of the distribution of the vibrissae in the various representatives of the family Didelphidae examined is given in Table 1.

In the active arboreal genera (*Didelphis*, *Metachirus*, *Marmosa* and *Dromiciops*) the full complement of vibrissae is retained in a highly developed state. In *Peramys*, which is said to be probably far less arboreal than the other didelphids (Thomas, 1888, p. 354), there is less development of the vibrissae on the limbs, although some of the facial groups show characteristics which are common to the family. The mystacial vibrissae are well developed and arranged in five or six principal longitudinal rows (Pl. 1, A and Fig. 2, A). The numerical constancy of the upper rows of these vibrissae is very marked, especially in *Didelphis*, *Metachirus* and *Marmosa* (Table 1). In all genera examined the superior mystacial row (Fig. 2, A) contains three vibrissae. The genal group is well developed and gives rise to from six to ten strong vibrissae except in *Peramys* and *Chironectes*, which have four or five. There are two supraorbital vibrissae in all genera except *Peramys* which has only one on each side. The vibrissae of the interramal group (except in *Chironectes*) show a remarkable uniformity in their arrangement. Typically, this group

TABLE 1

Distribution of the vibrissae in the Didelphidae

Species and number of specimens examined	Mystacial*					Genal	Supra-orbital	Inter-ramal	Sub-mental	Ulnar carpal	Medial ante-brachial	Anco-neal	Calca-neal
	Row 1	Row 2	Row 3	Row 4	Row 5								
Didelphis marsupialis Linn. var. (9)	3	3	5	6–7	7–8	7–10	2	5–6	4–5	3–6	1–2	0	0
Didelphis marsupialis var. *azarae* Temm. (2)	3	3	5	6	7–8	6–7	2	4–5	5–6	5–7	1	0	0
Metachirus opossum (Linn.) (1)	3	3	5	6	8	7	2	6	5–6	5–6	1	0	0
Marmosa cinerea Temm. (3)	3	3	5	6	7	8	2	4–5	3	2–3	1–2	0–1	0–1
Marmosa murina Linn. (1)	3	3	5	6	6–7	7	2	4	2	2	1	1	0
Dromiciops australis (Phillipi) (1)	3	4	6	6	7	6	2	5	3–4	3–4	2	0	1
Peramys dimidiatus Wagn. (1)	3	3	4	6	6–7	5	1	5	3	0–1	0	0	0
Chironectes minimus (Zimm.) (2)	3	2	3–5	5	5–6	4–5	2	11–12	7–10	2–4	0	0	0

* Mystacial vibrissae below row 5 not included.

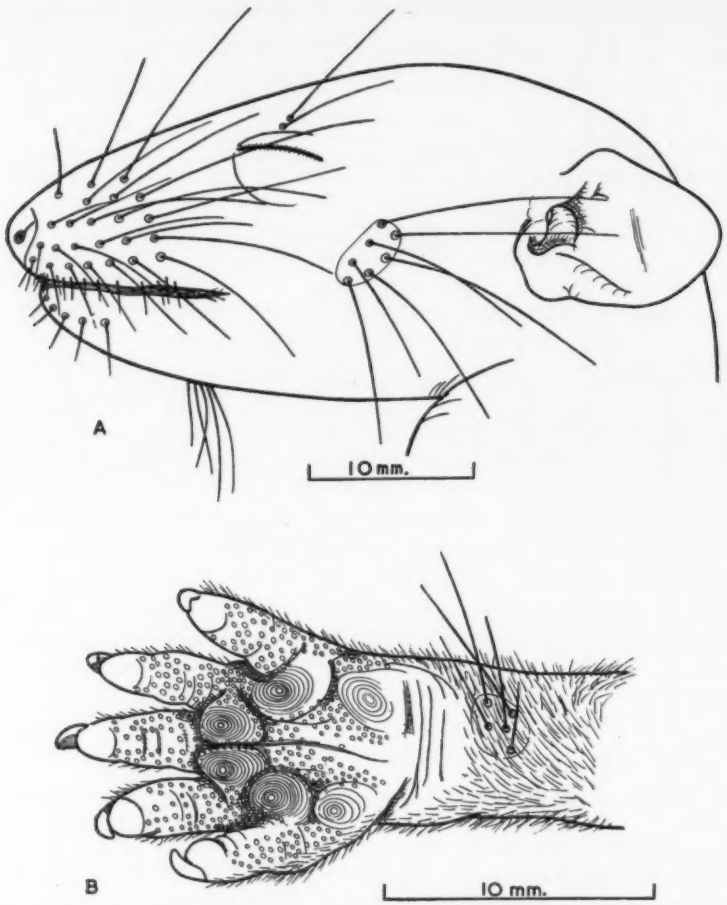


Fig. 2.—*Didelphis marsupialis* Linnaeus. Univ. Mus. Zool. Camb. A4. 9/14–15. A, male, facial vibrissae ; B, female, left manus, palmar aspect to show the ulnar carpal vibrissae.

contains five vibrissae (Fig. 3, A), an anterior one on the midline and two pairs behind. The anterior vibrissa may be absent or paired. When paired, the vibrissae may be arranged one behind the other on the midline, or side by side one on either side of the midline. In *Chironectes* the interramal papilla is extremely well developed and it gives rise to eleven or twelve strong vibrissae. Submental vibrissae (Fig. 3, A), represented in all the didelphids examined, are best developed in *Chironectes*. Ulnar carpal vibrissae (Fig. 2, B) are better developed in *Didelphis* and *Metachirus* than in *Peramys* and *Chironectes*, the only didelphids examined which are without other forearm vibrissae.

Medial antebrachial vibrissae are present in all except two genera and anconeal vibrissae are present only in *Marmosa*. Calcaneal vibrissae (Fig. 3, B), similar to those found in the Australian Phalangeridae, are present in two of the species examined (see Table 1).

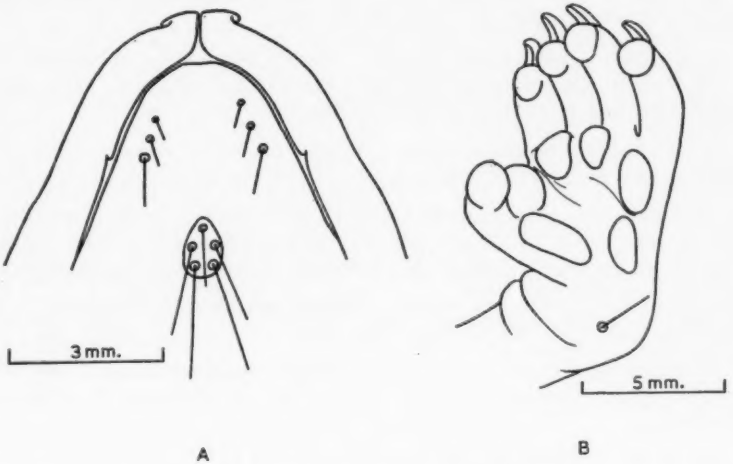


Fig. 3.—*Marmosa cinerea* Temminck. Univ. Mus. Zool. Camb. A4. 21/6 ; male. A, submental and interramal vibrissae. B, left pes showing calcaneal vibrissa.

Thomas (1888, pp. 368–69) referred to the various groups of facial vibrissae in *Chironectes minimus* but made no attempt to count the actual number of vibrissae in each group. *Chironectes*, the only truly aquatic marsupial, differs from the other didelphids examined in the better development of the interramal and submental vibrissae ; its interramal group of vibrissae is extremely well developed compared with those found in the remainder of the family.

The vibrissae of several juvenile specimens of *Didelphis marsupialis karkinophaga* Zimmermann were briefly described by Hill (1951). In agreement with the representatives of the genus *Didelphis* described above, all the typical groups of facial vibrissae were present, but no anconeal or calcaneal vibrissae were described.

Family II. **Dasyuridae** (Pl. 1, B and Figs. 4–5)

Material

1. *Antechinus swainsonii* (Waterhouse). Swainson's marsupial mouse. Five adults. X371, male (H+B 163) ; Sandy Bay, Tasmania. X445 and X446, two males (H+B 152) ; Maatsuyker Island, Tasmania. Nat. Mus. Vict.—two specimens, no register number and no data ; male (H+B 147) and female (H+B 142).

2. *Antechinus* (=*Pseudantechinus*) *macdonnellenses* (Spencer). Fat-tailed marsupial mouse.

C.492—adult male (H+B 106) ; Central Australia.

3. *Phascogale tapoatafa* (Meyer). Brush-tailed marsupial rat.

Two adults from Victoria. R. 4349. Male (H+B 231) from Monbulk and R. 7707 female (H+B 180) from Mt. Yule.

4. *Dasycercus cristicauda* (Krefft). Crest-tailed marsupial mouse.

Two adults from Charlotte Waters, Central Australia. R. 12411 female (H+B 175) and R. 12412 male (H+B 210).

5. *Dasyuroides byrnei* Spencer. Byrne's marsupial mouse. Two adults from Central Australia. C.456 male (H+B 168) and C.462 female (H+B 177).

6. *Sminthopsis crassicaudata* (Gould). Fat-tailed marsupial mouse.

Four adults from Deniliquin, N.S.W. R. 12751 female (H+B 86), R. 12761 male (H+B 79), R. 12768 male (H+B 80) and R. 12771 female (H+B 76).

7. *Sminthopsis leucopus* (Gray). White-footed marsupial mouse.

Adult male. 568 (H+B 105). No data.

8. *Antechinomys spenceri* Thomas. Jerboa marsupial mouse. Two adults from Central Australia. R. 12620 female (H+B 101) and R. 13208 male (H+B 78).

9. *Dasyurus quoll* (Zimmermann). Native cat.

Three pouch-young. A6. 11/15 male (H+B 67), no data. Tas. Mus.—two specimens from Huonville, Tasmania ; 207 (1) male (H+B 63) and 207 (2) sex ? (head length 17·5 mm.) probably litter mates.

10. *Dasyurops maculatus* (Kerr). Tiger cat.

Adult female from Arthur Lakes, Tasmania. Zool. Dept., University of Tasmania—no register number (H+B 400).

11. *Sarcophilus harrisii* (Boitard). Tasmanian devil.

Eight pouch-young (three males (H+B 107 to 222) and five females (H+B 112 to 162)) and one adult (female, H+B 560) from Tasmania. The largest male pouch-young belongs to the author's collection and the remainder are in the Tas. Mus.

12. *Thylacinus cynocephalus* (Harris). Tasmanian tiger. Four pouch-young from Tasmania. Two males ; 588 (H+B 140) and 589 (H+B 130). No data. Two females, litter mates ; R. 3025 (H+B 126) and R. 3027 (H+B 130).

The vibrissae in some of the Dasyuridae have been described by Pocock (1914, 1926), Wood Jones (1923b, 1923d), Carlsson (1926), Boardman (1945) and Hill (1951).

In the course of the present investigation, the vibrissae of several species have been re-examined and those of several other species are described for the first time. A summary of the distribution of the vibrissae in the various representatives of the family Dasyuridae examined is given in Table 2.

Distribution of the vibrissae in the Dasyuridae

Species and number of specimens examined	Mystacial*				Genal	Supra-orbital	Inter-ramal	Sub-mental	Ulnar carpal	Medial ante-brachial	Anconeal
	Row 1	Row 2	Row 3	Row 4							
Antechinus swainsonii (Waterh.) (5)	4	6–9	7–10	10	9–11	1–2	3–5	3–9	0–6	0–1	0–1
Antechinus macdonnellensis (Spencer) (1)	4	5	6	8	11	2	4	3–4	6	2	1
Phascogale tapoatafa (Meyer) (2)	4	6–7	9–10	9–10	10–12	2–3	2	5–6	5–8	1	1
Dasycercus cristicauda (Krefft) (2)	4–5	5–6	6–7	8	9–10	2	4	4–6	5–7	0–1	0
Dasyuroides byrnei Spencer (2)	3–4	5	7	7–8	9–10	2	2–4	4–6	5–7	1	0
Sminthopsis crassicaudata (Gould) (4)	—	—	—	—	7–10	2	2–4	4–5	2–3	1	0
Sminthopsis leucopus (Gray) (1)	4	7	7–8	8	8–9	2	4	3 ?	1–3	1	0
Antechinomys spenceri Thomas (2)	2	4	2	5	6	2–3	1–2	3–4	4	0	0
Dasyurus quoll (Zimm.) (3)	2	4	6	7–9	7–8	3–4	3–4	7	4–6	0–1	0–1
Dasyurops maculatus (Kerr) (1)	4	5	6–7	9–10	10–11	3–4	3	6–7	6–10	2	0
Sarcophilus harrisii (Boitard) (2)	2–4	4–5	5–7	7–8	15–23	6–7	9–23	—	10–12	0	0
Thylacinus cynocephalus (Harris) (4)	2	3	4–5	5	5–8	5–8	10–11	13–16	0	0	0

* Mystacial vibrissae below row 4 not included.

In *Dasyurus*, *Dasyurops*, *Sarcophilus* and *Thylacinus*, Pocock (1914) has pointed out the invariable occurrence of the mystacial, genal, supraorbital and interramal groups. These facial groups, as well as the submental group, are present in all the dasyurids so far examined (Table 2).

The mystacial vibrissae (Pl. 1, B and Figs. 4–5) are usually extremely well developed and arranged in five to eight principal rows. In addition, there is a number of smaller mystacial vibrissae near the margin of the upper lip. In *Thylacinus* the mystacial vibrissae are arranged in five principal rows. Above

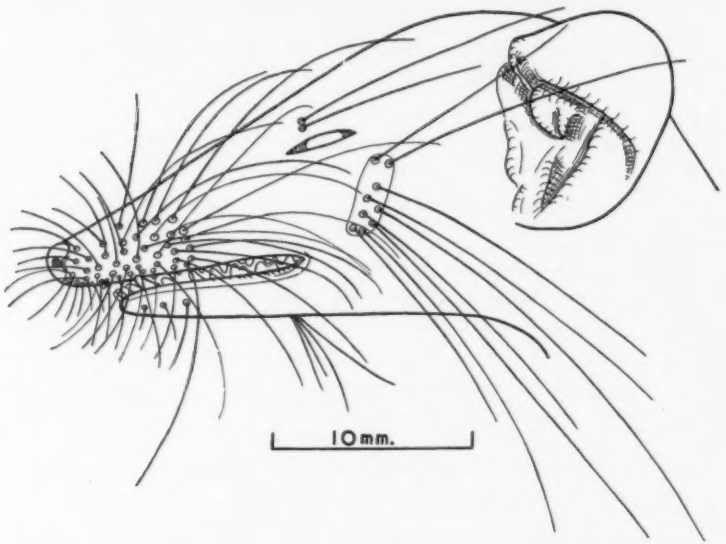


Fig. 4.—*Sminthopsis leucopus* (Gray). Tas. Mus. 568, adult male. Facial vibrissae.

the principal rows, Boardman (1945) describes " three further rows consisting each of only a single vibrissa placed towards the caudal margin of the mystacial zone ". In all the specimens of *Thylacinus* examined (including two of those examined by Boardman) there are five vibrissae above the five principal rows (Fig. 5, B). These five vibrissae represent two rows; a superior one containing two vibrissae and a second one containing three vibrissae. The most superior of the principal rows is here defined as row three instead of row four used by Boardman. In *Sminthopsis crassicaudata* the mystacial vibrissae are extremely well developed but no attempt was made to count the actual number of vibrissae present in each row.

The genal group of vibrissae is extremely well developed, especially in *Sarcophilus* (Pl. 1, B and Fig. 5, A) where there are fifteen to twenty-three strong vibrissae arising from a large protuberance. The best development of supraorbital vibrissae is found in the large dasyurids ; *Sarcophilus* and *Thylacinus* (Figs. 5, A and 5, B). In the former the vibrissae are very strong.

In the small marsupial mice (e.g. *Sminthopsis leucopus* shown in Fig. 4) the supraorbital group usually has two strong vibrissae but it may contain one or three vibrissae. In *Dasyurus* the exact number of supraorbital vibrissae is difficult to determine because of the early development of pelage hairs.

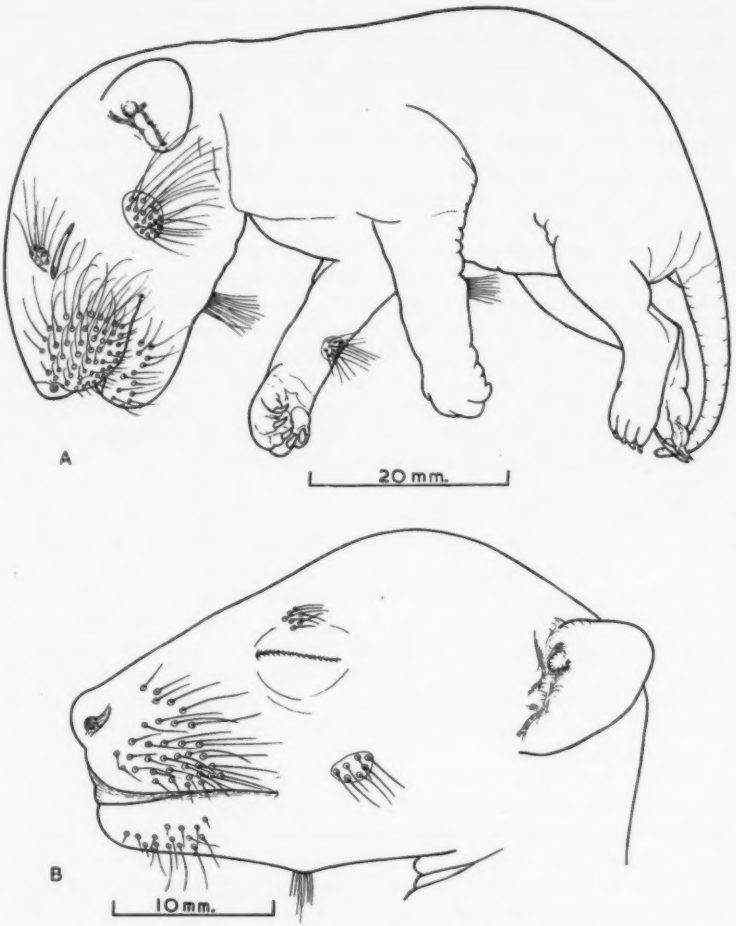


Fig. 5.—A, *Sarcophilus harrisii* (Boitard). Tas. Mus. 586 (B), female pouch-young. General form to show the distribution of all the vibrissae. B, *Thylacinus cynocephalus* (Harris). Tas. Mus. 589, male pouch-young. Facial vibrissae.

The interramal vibrissae, like the supraorbitals, are most numerous in *Sarcophilus* and *Thylacinus* (Figs. 5, A and 5, B). In *Antechinus swainsonii* the interramal set is well developed with three to five strong vibrissae arising

from the papilla. When four interramals are present they arise at the corners of a square. When five are present the fifth one is placed on the midline immediately in front of the group of four. It is interesting to compare this arrangement with that usually found in the didelphids (see Fig. 3, A for *Marmosa cinerea*). In *A. macdonnellensis* and *Dasycercus cristicauda* the interramal vibrissae are arranged at the corners of a square in a manner similar to that described for *A. swainsonii*.

The submental vibrissae are usually pale and not well defined. They are numerous in *Sarcophilus* (Fig. 5, A) and *Thylacinus* (Fig. 5, B) but no attempt was made to count the exact number in the former.

In addition to a full set of facial vibrissae, all the dasyurids except *Thylacinus* have ulnar carpal vibrissae. Medial antebrachial or anconeal vibrissae or both are present in all except the specialized genera *Antechinomys*, *Sarcophilus* and *Thylacinus*.

In *Thylacinus* the development of the vibrissae is poor, especially when compared with that in the small Australian polyprotodonts. Pocock (1926, p. 1039) considered that the vibrissae of *Thylacinus* show an adaptive approximation to those of the Canidae, except that in the latter there are always two genal groups on the cheek, one set high above the other. Although in *Thylacinus* the vibrissae in most of the facial groups are not reduced in number, they are poorly developed in length and thickness as compared with those of other Dasyuridae. It is only in *Sarcophilus* that a greater number of vibrissae is found in several of the facial groups (see Table 2).

Thylacinus is unique among the dasyurids in not having vibrissae on the fore-limb (Table 2). It is this character rather than, as Pocock (1926, p. 1039) thought, the reduction in facial vibrissae, that can probably be explained by its mode of life. *Thylacinus*, a digitigrade cursorial predatory dasyurid, captured its prey to a great extent by its speed in open country, where tactile vibrissae on the fore-limb would not be especially useful. *Sarcophilus*, on the other hand, is not specialized for digitigrade gait and does not frequent open country to the same extent as did *Thylacinus*. *Sarcophilus* shows a great contrast to *Thylacinus* in the development of a strong ulnar carpal group of vibrissae and in the stronger development of the facial groups, particularly the genal and interramal sets.

Carlsson (1926) referred briefly to the vibrissae of several representatives of the subfamily Phascogalinae. She found that the mystacial and genal vibrissae are particularly long and numerous in *Dasyuroides byrnei*, *Antechinus flavipes* (Waterhouse), *Sminthopsis crassicaudata* and *Antechinomys spenceri*. On the other hand she found that the submental and interramal vibrissae are short and sparse in *Phascologale* (=*Antechinus*) and *Sminthopsis*, while in *Dasyuroides* and *Antechinomys* they are represented by only a few hairs. Carlsson referred to the presence of ulnar carpal vibrissae in all the Dasyuridae she examined, but made no reference to other forearm vibrissae.

In the course of the present investigation *Antechinus flavipes* has not been examined but two related species *A. swainsonii* and *A. macdonnellensis*, as well as *Dasyuroides*, have been studied. There is no marked difference between these species in the number of submental and interramal vibrissae.

In Wood Jones' (1923b) description of the vibrissae in pouch-young of *Dasycercus cristicauda* no mention is made of any papillae or vibrissae on the forearm other than those of the ulnar carpal group.

Family III. **Myrmecobiidae** (Fig. 6)

Material

1. *Myrmecobius fasciatus* Waterhouse. Numbat or marsupial ant-eater. A6. 37/6—adult female (H+B 245) ; River Murray, South Australia.

Myrmecobius fasciatus is the only representative of the family Myrmecobiidae. In the solitary specimen examined (Fig. 6) the mystacial group is greatly reduced ; there are only nine vibrissae on the right side and ten on the left side, with little or no arrangement in rows. The genal group is extremely well developed but the exact number of vibrissae cannot be determined. This group is situated directly below the eye and contains about ten large vibrissae, in addition to a number of smaller ones. In addition there are several vibrissae on or near the lower eyelid which may belong to the genal group or represent a separate suborbital set. The supraorbital papilla, situated above the anterior (medial) canthus, gives rise to two strong vibrissae. The interramal papilla, placed on a line joining the angles of the mouth, gives rise to two pale backwardly directed vibrissae. The submental group, like the mystacial, is poorly developed, there being only one vibrissa on the left side and two on the right side. Only one ill-defined ulnar carpal vibrissa can be detected on each forearm. No calcaneal or other vibrissae are discernible.

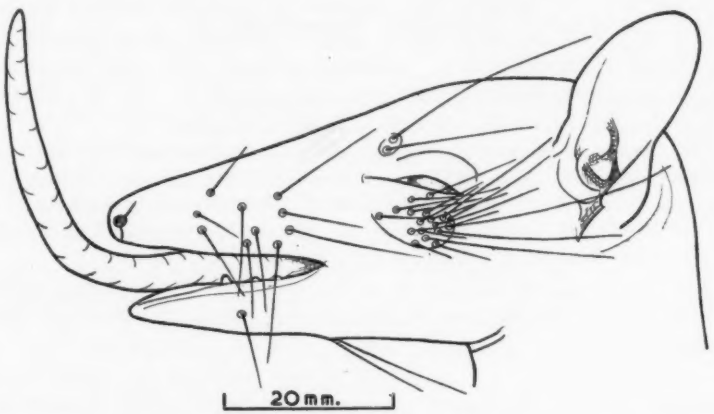


Fig. 6.—*Myrmecobius fasciatus* Waterhouse. Univ. Mus. Zool. Camb. A6. 37/6, female. Facial vibrissae.

The distribution of the vibrissae in pouch-young of *M. fasciatus* (Wood Jones, 1923c, p. 199) is similar to that found in the adult specimen described above. In reference to the mystacial set present in pouch-young, Wood Jones says that it " consists of a few irregular vibrissae which do not arise in any

recognizably ordered manner. Most of the individual bristles are not straight, as such sensory vibrissae usually are, but are waved in direction ".

Pocock (1926, pp. 1040–41) described the facial vibrissae in the adult animal and he too found that the mystacials are greatly reduced in number and length, a condition which is common to all the ant-eating mammals (Pocock, 1914). Pocock (1926, pp. 1040–41) said that the interramal vibrissae of *Myrmecobius* are altogether suppressed but this is not the case in the specimen described above, or in the juvenile specimens described by Wood Jones. However, Wood Jones said that the interramals, together with the submentals, soon lose their identity and merge with the coarse pelage hairs. Pocock does not describe or figure any submental vibrissae.

The ulnar carpal set is better developed in juvenile specimens than it is in the adult animal. In the pouch-young described by Wood Jones, the ulnar carpal papilla gives rise to four vibrissae. With the development of the pelage hair on the forearm, the identity of the ulnar carpal vibrissae becomes lost. In his general description of the adult animal, Wood Jones (1923d, p. 125) said that " the ulnar carpal set is unrepresented ". In the adult specimen before me there is a solitary ill-defined ulnar carpal vibrissa on each forearm.

The poor development of brachial vibrissae is, no doubt, associated with the mode of life of this highly specialized unique marsupial. It is terrestrial in habit and does not excavate deep burrows or climb (Wood Jones, 1923d, p. 126).

Family IV. **Notoryctidae**

Material

1. *Notoryctes typhlops* (Stirling). Marsupial mole.

C.579—adult female (H+B 125) ; Central Australia.

The family Notoryctidae contains only a single remarkably specialized representative, *Notoryctes typhlops*. This unique animal is the only marsupial examined in which no sensory papillae or vibrissae can be detected. The absence of papillae and vibrissae in a 10 mm. pouch-young, and in the adult, has been described by Wood Jones (1921 ; 1923d, p. 129).

Notoryctes is almost completely subterranean in habit and it is probable that the deficiency of vibrissae in this animal is intimately associated with its unusual mode of life.

Family V. **Peramelidae** (Fig. 7)

Material

1. *Isoodon obesulus* (Shaw and Nodder). Short-nosed bandicoot.

Fifteen pouch-young from Tasmania, one pouch-young from Central Australia and two adults from Victoria. Ten of the pouch-young are in the Tas. Mus. and five belong to the author's collection. The remainder, the specimen from Central Australia, and the two adults, are in the Nat. Mus. Vict.

2. *Perameles nasuta* Geoffroy. Long-nosed bandicoot.

Sixteen pouch-young (eight males and eight females) from New South Wales. One specimen (H+B 142) was examined at the Prosectorium, Zool. Soc. Lond. The remainder (H+B 58 to 94) are in the Embryology Department, University College, London (Prof. J. P. Hill Collection). The specimen at the Prosectorium, although described elsewhere (Hill, 1951, p. 158), has been re-examined in order to make a more detailed study of the distribution of the vibrissae.

3. *Perameles eremiana* Spencer. Desert bandicoot.

Two female pouch-young (H+B 95) of the same litter ; Central Australia. Registration numbers are the same for both specimens, namely C.488.

4. *Perameles gunnii* Gray. Tasmanian and Victorian barred bandicoot.

Thirty-four specimens ; twenty-two pouch-young (H+B 80–145) and seven adults (H+B 240–330), from Tasmania ; remainder, all pouch-young (H+B 110–140), from Victoria. The Victorian specimens are in the Nat. Mus. Vict., one of the Tasmanian specimens is in the Tas. Mus., and the remainder belong to the author's collection.

5. *Perameles myosura* Wagner. Western barred bandicoot.

R.13019—female (H+B 185) ; Western Australia.

6. *Macrotis lagotis* (Reid). Rabbit bandicoot or bilby.

Two pouch-young and two adults. (a) Zool. Soc. Lond. M8—male pouch-young (H+B 68) ; no data. (b) Nat. Mus. Vict.—three specimens from Central Australia ; C.594, female pouch-young (H+B 95) ; R.13505, adult female (H+B 325) ; R.13506, adult female (H+B 340).

7. *Macrotis minor* (Spencer). Lesser rabbit bandicoot.

Three specimens from Central Australia ; R.12313, type specimen, adult female (H+B 220) ; R.12431, male pouch-young (head length 35·5 mm.) ; R.12434, adult female (H+B 195).

8. *Choeropus* (=*Chaeropus*) *ecaudatus* (Ogilby). Pig-footed bandicoot.

Four specimens from Central Australia ; C.469, adult male (H+B 270) ; R.12406, female (H+B 185), R.13045, adult female (H+B 300) ; R.13046, female pouch-young (H+B 94).

The vibrissae of a number of Australian peramelids have been described by Wood Jones (1922a), Boardman (1943), Hill (1951) and Lyne (1951, 1952). In the course of the present investigation, the vibrissae of several species have been re-examined, and those of two species, *Perameles myosura* and *Macrotis minor*, are described for the first time.

A summary of the distribution of the vibrissae in the Peramelidae which have been examined in the present investigation is shown in Table 3. The distribution of the vibrissae in seven Australian species, including *Isoodon barrowensis*, described by Wood Jones (1922a), and *Perameles nasuta*, described by Boardman (1943), were summarized by Lyne (1952, pp. 647–48).

All the typical facial groups of vibrissae are usually represented. The mystacial vibrissae (Fig. 7, A, B and C) are usually arranged in six well-defined rows. In *Macrotis lagotis* and *M. minor* several longish hairs, which

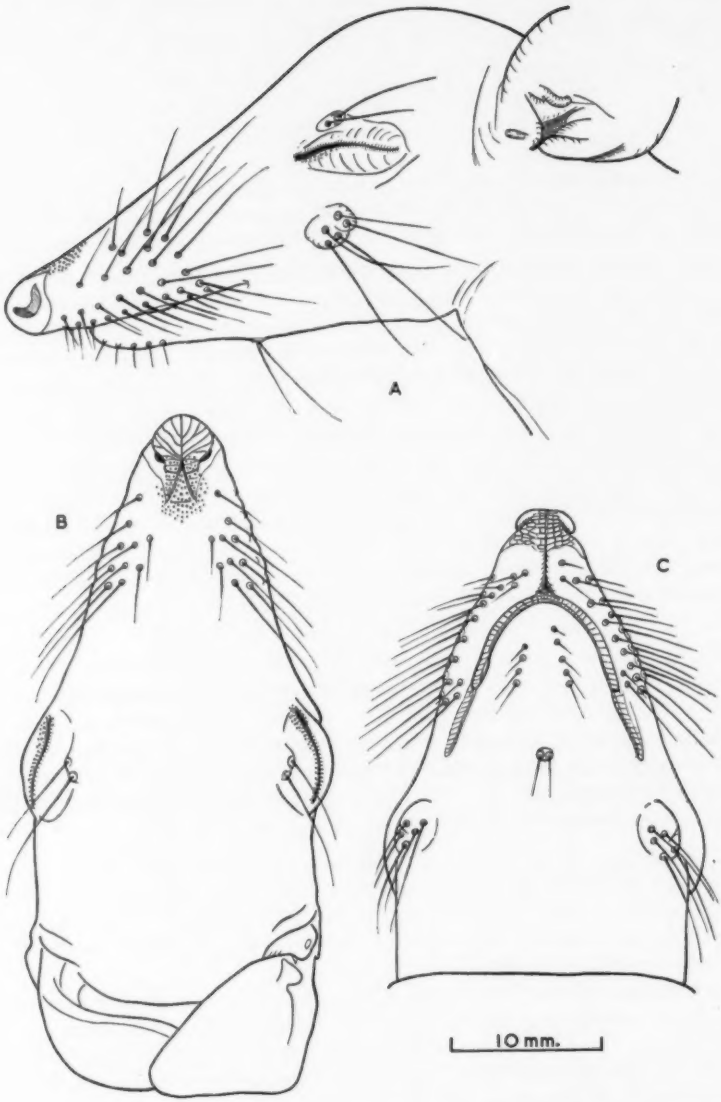


Fig. 7.—*Perameles gunnii* Gray. × 182, female. Facial vibrissae. A, lateral view. B, dorsal view. C, ventral view.

may or may not be vibrissae, are situated below the sixth row. The vibrissae of the three upper rows are usually darker than those of the lower rows. Rows three and four usually diverge towards the point of the snout (Fig. 7, A). The most notable feature of the mystacial vibrissae in several species is the numerical constancy of several of the upper rows. Note particularly the constancy of row two in *I. obesulus* and rows two and three in *P. nasuta* (Table 3).

The vibrissae of the genal group (Table 3) exhibit a remarkable numerical constancy in several species.

With the exception of one specimen of *Perameles gunnii*, all the peramelids examined, except *Choeropus*, have two supraorbital vibrissae. In *Choeropus* the supraorbital set is reduced to a solitary vibrissa. The number of interramal vibrissae is usually not constant and in one species, *Macrotis minor*, there is no trace of this group. In another species, *Perameles eremiana*, there is a solitary hair which may or may not be an interramal vibrissa. In a third species, *Macrotis lagotis*, the interramal group cannot be detected in one of the four specimens examined. In a fourth species, *Perameles myosura*, the interramal area was overlooked in the only specimen examined, but as Wood Jones (1924c, p. 148) makes no reference to interramal vibrissae in this species, they are probably absent.

As a rule, the submental group is best developed in the genus *Perameles* (see Table 3), and is present in all species except *Macrotis lagotis*.

On the forearm, the ulnar carpal papilla is always represented and it usually gives rise to three vibrissae, although in *Choeropus* the set is reduced to a solitary vibrissa.

The anconeal group, represented by a solitary vibrissa in *Isoodon obesulus* and *I. barrowensis* (Wood Jones, 1922a), has not been described in other Australian peramelids. Probably this group is represented in many of the peramelids recorded from the islands north of Australia.

Of the bandicoots so far examined, it is only in the highly specialized genus *Choeropus* that one finds a great reduction of the sensory vibrissae (see Table 3). This agrees with Pocock's (1914) earlier findings in his examination of a large number of mammals. He remarked that " in a great many cases, within the limits of a single order, the species which are defective in the matter of vibrissae are the higher derivative types, whereas those in which all or most of them are present are more generalised types ".

Family VI. **Caenolestidae** (Fig. 8)

Material

1. *Caenolestes fuliginosus* (Tomes).

Zool. Soc. Lond.—two adults ; 150317, males (H+B 130) and 150318, female (H+B 115) ; vicinity of Quito, Ecuador.

2. *Orolestes inca* Thomas.

B.M.—two adult males ; 194927 (H+B 108) and 194940 (H+B 112) ; 1914–1915.

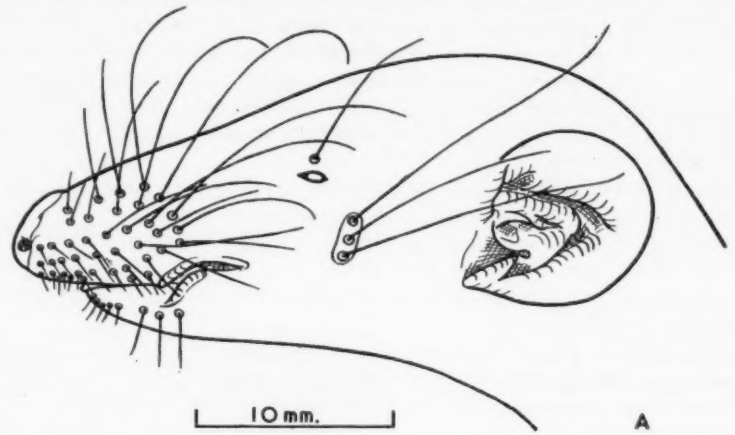
TABLE 3

Distribution of the vibrissae in the Peramelidae

Species and number of specimens examined	Mystacial						Genal	Supra-orbital	Inter-ramal	Sub-mental	Ulnar carpal	Anco-neal
	Row 1	Row 2	Row 3	Row 4	Row 5	Row 6						
Isoodon obesulus (Shaw and Nodder) (18)	1–2	2	4–5	3–5	4–8	1–3	7	2	2–5	2–4	3–4	1
Perameles nasuta Geoffroy (16)	3–4	4	6	7–9	5–10	3–6	6–7	2	2–4	3–7	3	0
Perameles eremiana Spencer (2)	2	4	6	6–7	8–9	4–5	5	2	1 ?	4–5	3	0
Perameles gunnii Gray (34)	2–4	3–4	5–6	6–8	9–14	1–3	4–6	2–3	1–4	4–8	3	0
Perameles myosura Wagner (1)	2	4	6	6	7	3	5	2	—	4	3	0
Macrotis lagotis (Reid) (4)	3	4	5–6	6–8	6–10	4–6	5–7	2	0–2	0	3–4	0
Macrotis minor (Spencer) (3)	2–4	4	5	7	9	4–6	5–6	2	0	1–2	3	0
Choeropus ecaudatus (Ogilby) (4)	1–2	2–3	4	4	4–8	2–3	3	1	1	1–2	1	0

The mystacial vibrissae are arranged in five principal longitudinal rows and there is, in addition, a number of small vibrissae near the margin of the upper lip (Fig. 8, A). Row one has three or four vibrissae, row two has five or six, row three has seven or eight, and row four has eight or nine. The mystacials below row four have not been counted.

The genal papilla gives rise to three or four strong vibrissae, and the supraorbital group is represented by a solitary vibrissa (Fig. 8, A). In neither



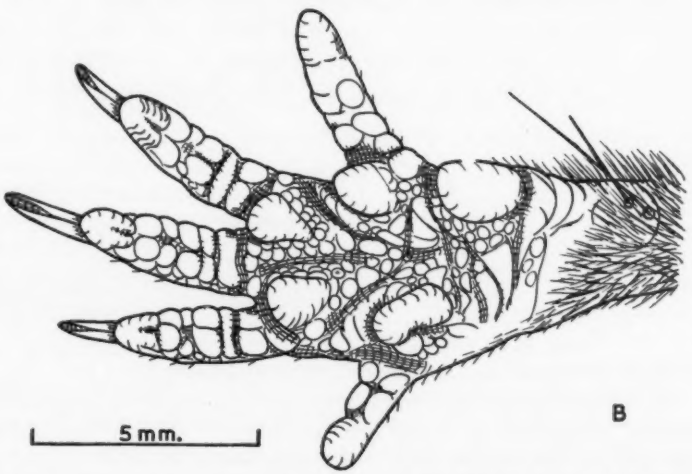


Fig. 8.—*Caenolestes fuliginosus* (Tomes). Zool. Soc. Lond. 150318, female. A, facial vibrissae. B, left manus, palmar aspect to show the ulnar carpal vibrissae.

species is there any sign of interramal vibrissae. The submentals are represented by several vibrissae on each side of the chin. Of the forearm vibrissae only the ulnar carpal group (Fig. 8, B) is present. In *Caenolestes fuliginosus* there appear to be two or three ulnar carpals in the female, but they were not counted in the male. In *Orolestes inca* one specimen has three ulnar carpal vibrissae on each side and the other specimen has two on one side and one on the other.

Osgood (1921), in a lengthy monograph on *Caenolestes*, figures the distribution of the vibrissae but did not describe them in the text. Pl. 1 of his monograph shows an adult *Caenolestes* with at least one supraorbital vibrissa and Pl. 2, Fig. 1 shows the right side of an adult head without supraorbital vibrissae. In the specimens of *Caenolestes fuliginosus* and *Orolestes inca* examined in the present investigation, the supraorbital group is represented by a solitary vibrissa.

Osgood (Pl. 2, Fig. 1) shows only two groups of facial vibrissae ; a strong mystacial group and a smaller but distinct genal group containing four vibrissae. The specimens of *Caenolestes fuliginosus* and *Orolestes inca* described in the present study have three and four genals respectively. In neither species can interramal vibrissae be detected but the submental group is represented in all specimens examined.

Osgood (Pl. 2, Fig. 4) shows an ulnar carpal group of four strong vibrissae. In the caenolestids described in the present investigation the exact number of ulnar carpal vibrissae is difficult to determine. There appear to be two or three in one specimen of *Caenolestes fuliginosus* and one to three in *Orolestes inca*.

The absence of other brachial vibrissae is probably associated with the mode of life of these unusual marsupials. According to Osgood (1921, p. 17) " Caenolestes is of terrestrial and crepuscular or nocturnal habits ".

Suborder DIPROTODONTIA

Family I. **Phalangeridae** (Pls. 2 and 3 and Figs. 9–14)

Material

1. *Tarsipes spenserae* Gray. Honey possum.

Nat. Mus. Vict., and Univ. Mus. Zool. Camb.—five adults (H+B 82–95) and one pouch-young (H+B 44) ; Western Australia.

2. *Acrobates pygmaeus* (Shaw). Pigmy glider.

Nat. Mus. Vict.—five adults (H+B 65–80) from Deniliquin, N.S.W. Author's collection—one pouch-young (H+B 34) from Woore Yallock, Victoria.

3. *Cercartetus nanus* (Desmarest). Pigmy possum.

A9. 44/6 juvenile male (H+B 61) and A9. 44/7, juvenile female (H+B 65) from Australia. X574, adult male (H+B 90·5) from Fern Tree, Tasmania.

4. *Eudromicia lepida* (Thomas). Tasmanian pigmy possum.

Nine specimens (H+B 50–87) from Tasmania. Department of Zoology, University of Tasmania, one female ; Tas. Mus., five females and three males.

5. *Petaurus australis* Shaw and Nodder. Yellow bellied glider.

C.763, male (H+B 308) ; Portland, Victoria.

6. *Petaurus breviceps* Waterhouse. Sugar glider.

Seven specimens. Nat. Mus. Vict.—four adults (one male and three females) from Victoria. Tas. Mus.—one female pouch-young from Tasmania. Author's collection—two adult males.

7. *Pseudocheirus convolutor* (Oken). Tasmanian ring-tail.

One hundred and twenty-three pouch-young (sixty males and sixty-three females) from Tasmania. Eighty-one specimens belong to the author's collection. The remainder are in the Tas. Mus.

8. *Schoinobates volans* (Kerr). Greater possum-glider.

Two pouch-young. C.670, female (H+B 145) from Victoria. Embryology Department, University College, London (Professor J. P. Hill collection).—male (H+B 138).

9. *Trichosurus vulpecula* (Kerr). Brush-tailed possum.

One hundred and six pouch-young from Tasmania and one pouch-young from Western Australia. Sixty-six specimens belong to the author's collection. The remainder are in the Tas. Mus.

The vibrissae of a number of representatives of the subfamily Phalangerinae have been previously described. The vibrissae of *Trichosurus vulpecula* (Kerr) have been described by Broom (1899), Pocock (1914), Wood Jones (1920), Gibbs (1938) and Hill (1951). In another paper on the external characters of pouch-young of marsupials, Wood Jones (1922b) described the distribution of the vibrissae in *Pseudochirops* (=*Petroseudes*) *dahli* (Collett). Also, Wood Jones (1924c) has briefly described the vibrissae in four other phalangers, namely :—*Acrobates pygmaeus* (Shaw), *Pseudocheirus laniginosus* (Gould), *Cercartetus concinnus* (Gould) and *Petaurus breviceps* Waterhouse. Pocock (1914) and Hill (1951) briefly referred to the vibrissae of *Pseudocheirus peregrinus* (Boddaert) and *Acrobates pygmaeus* (Shaw) respectively. Hill (1951) also briefly described the vibrissae of *Schoinobates volans* (Kerr) and *Pseudocheirus laniginosus* (Gould).

A summary of the distribution of the vibrissae in the Phalangeridae examined is shown in Table 4. Only those species examined in the course of the present investigation are shown in this table.

In one species, *Trichosurus vulpecula* (Pl. 3 and Figs. 13–14), all the typical groups of vibrissae are nearly always represented. In another species, *Tarsipes spenserae* (Fig. 9), all the typical groups may be present or the interramal and anconeal groups may be missing. A characteristic feature of many of the phalangers is the absence of the interramal group. Only in two species (see Table 4) of the various phalangers examined is the interramal group always present. In two other species the interramals may be absent or represented by a solitary vibrissa. In the remainder there is no trace of this group. Gibbs (1938) figures the interramal group of vibrissae in *Trichosurus vulpecula* but referred to them incorrectly as submental vibrissae. The submentals are situated further forward on either side of the chin and are quite distinct from the medially placed interramal papilla and its associated vibrissae. In all the

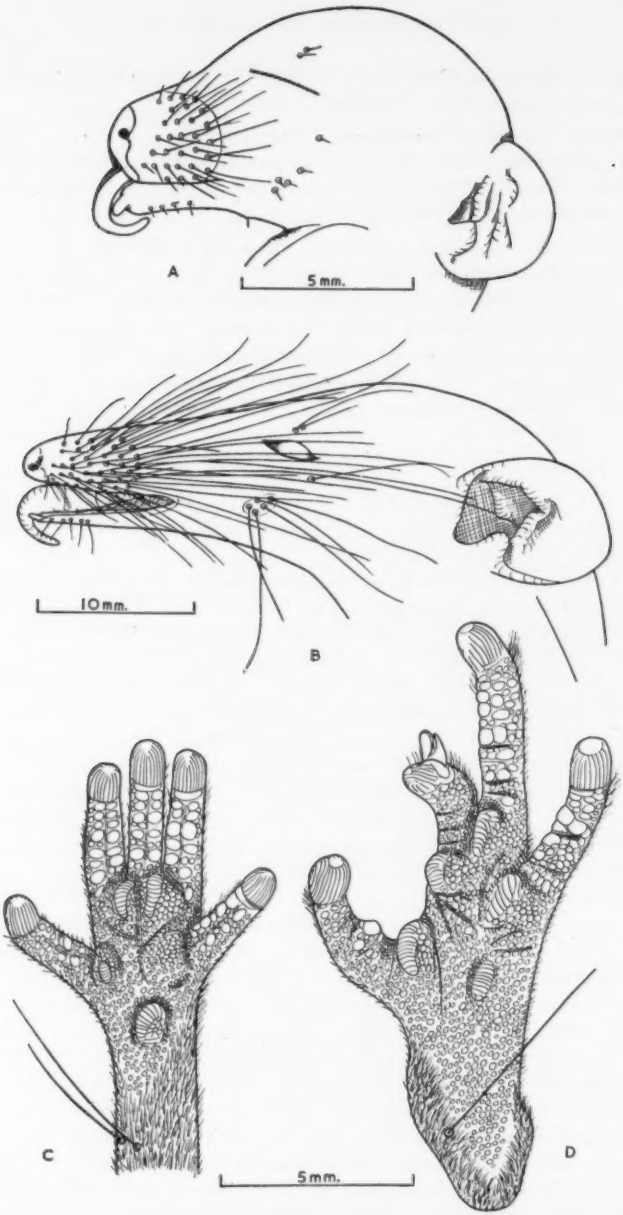


Fig. 9.—*Tarsipes spenserae* Gray. A and B, facial vibrissae. A, Univ. Mus. Zool. Camb. A9. 50/6, male pouch-young. B, Nat. Mus. Vict. R.12667, adult female. C, Univ. Mus. Zool. Camb. A9. 50/6, adult female. Left manus, palmar aspect to show the ulnar carpal vibrissae. D, same specimen as C. Left pes, plantar aspect to show the calcaneal vibrissa.

specimens of *Trichosurus vulpecula* examined (Table 4), and in the specimens described by other workers, all the typical sets of facial vibrissae are represented and well developed.

In reference to *Pseudocheirus peregrinus*, Pocock (1914) said that it differs from *Trichosurus vulpecula* in the lesser development of the interramals.

Hill (1951) in his description of several specimens of *Acrobates pygmaeus* said that both the interramal and submental groups are absent. In the specimens of this species examined in the present study the submental group is represented but there is no trace of interramal vibrissae. Hill said that the interramals are lacking in *Schoinobates volans*, and represented only by a papilla in *Pseudocheirus laniginosus*. Wood Jones (1924c), on the other hand, in his description of *Pseudocheirus laniginosus*, said that " all facial vibrissae are well developed " but he made no special reference to the interramal set. In any case, it appears that the interramals of *P. laniginosus*, are only poorly represented.

For *Cercartetus concinnus* and *Petaurus breviceps*, Wood Jones (1924c) said that all the typical facial groups of vibrissae are present. *C. concinnus* has not been examined in the present study but the related species *C. nanus* (Fig. 11) is without interramal vibrissae and none have been detected in *Petaurus breviceps*.

Acrobates pygmaeus (Pl. 2 and Fig. 10) is unique among the marsupials in not having supraorbital vibrissae. Wood Jones (1924c) in his description of this species said that all the vibrissae are extremely well developed but he

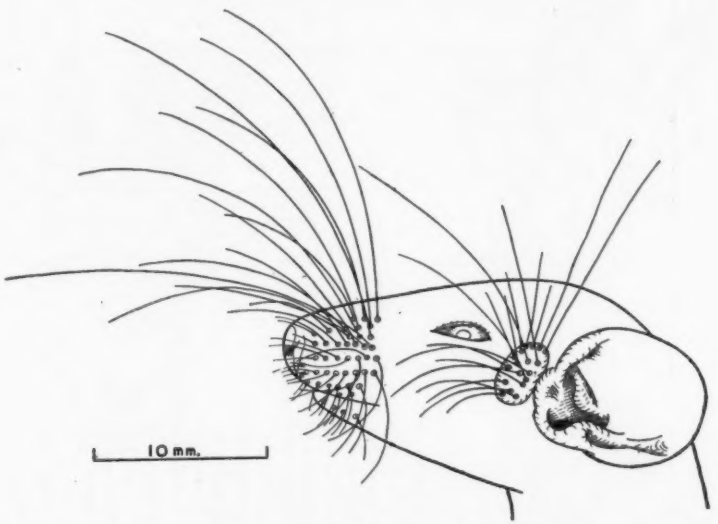


Fig. 10.—*Acrobates pygmaeus* (Shaw). Nat. Mus. Vict. R.8174, adult female. Facial vibrissae. Note the absence of supraorbital vibrissae and the strong development of the mystacial and genal groups.

TABLE 4

Distribution of the vibrissae in the Phalangeridae*

Species and number of specimens examined	Mystacial					Genal	Supra-orbital	Inter-ramal	Ulnar carpal	Medial ante-brachial	Anco-neal	Calca-neal
	Row 1	Row 2	Row 3	Row 4	Row 5							
Tarsipes spenserae Gray (6)	4–5	3–6	4–6	4–7	—	3–6	2	0–1	2	1–2	0–1	1
Acrobates pygmaeus (Shaw) (6)	2–3	4–6	3–4	7	6–7	16–20	0	0	3–4	0	0	1–2
Cercartetus nanus (Desmarest) (3)	4–5	5	6–7	—	—	4–5	2	0	3	1		1
Eudromicia lepida (Thomas) (9)	3–5	5–6	6–7	—	—	4–5	2–3	0	2–3	1–2		1
Petaurus australis Shaw and Nodder (1)	2	4	4–5	4	5	3	2	0	3–4	0	0	2
Petaurus breviceps Waterhouse (7)	2	2–4	2–3	4–6	—	2–3	2	0	2–5	0	0	1–3
Pseudocheirus convolutor (Oken) (123)	2–4	3–5	2–3	5–7	—	3–7	1–3	1–3	3–7	0–1	0	2–5
Schoinobates volans (Kerr) (2)	1–2	3	2	5	—	2–4	2	0–1	6–7	0–1	0	2
Trichosurus vulpecula (Kerr) (107)	2–4	5–7	6–10	—	—	3–8	1–3	2–4	8–15	0–5	0–2	0–4

* Submental and lower mystacial vibrissae not included.

made no reference to the complete absence of the supraorbital group or to the extraordinary development of the genal group. Also, the calcaneal group was not recognisable in the specimens of this species examined by Wood Jones. A group of two supraorbital vibrissae is characteristic of all the phalangers (except *Acrobates pygmaeus*) but one or three may be present (Table 4).

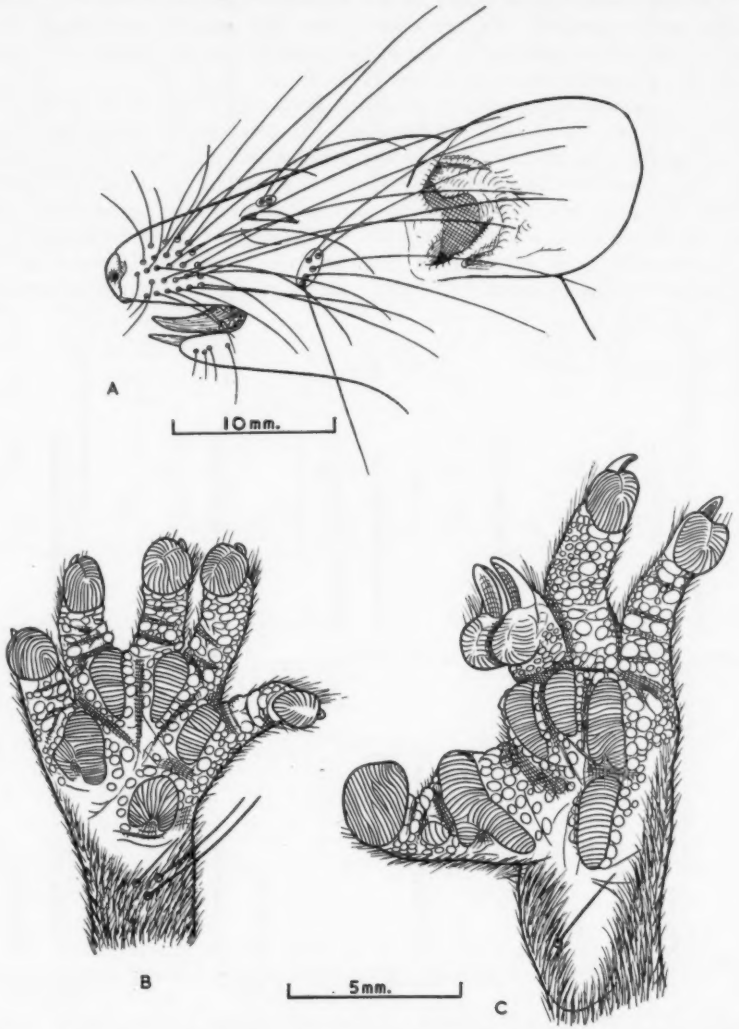


Fig. 11.—*Cercartetus nanus* (Desmarest). A, X574, adult male. Facial vibrissae. B and C, Univ. Mus. Zool. Camb. A9. 44/4, adult female. B, left manus, palmar aspect to show the ulnar carpal vibrissae. C, left pes, plantar aspect to show the calcaneal vibrissa.

The ulnar carpal group is represented in all the phalangers (see Table 4) and is best developed in *Trichosurus vulpecula* (Pl. 3, B).

Vibrissae on the fore-limb, other than the typical ulnar carpal group, are not found in volant phalangers, with one exception (see Table 4). In two phalangers, *Cercartetus nanus* and *Eudromicia lepida*, it is not known whether the vibrissae on the lateral aspect of the forearm represent the medial antebrachial or anconeal set. In two other species the medial antebrachial only may or may not be represented, and in two more species all groups of forearm vibrissae are usually represented (see Table 4).

The calcaneal group is present in all the phalangers examined (see Table 4).

Two species, *Pseudocheirus convolutor* and *Trichosurus vulpecula*, have been examined especially to discover any possible sex difference in the number and arrangement of the vibrissae. In *P. convolutor* (Fig. 12) no difference between the sexes can be detected but in two areas of *T. vulpecula* (Fig. 13), male specimens show a slight tendency to develop more vibrissae than do female specimens. In other areas, there is no obvious sex difference in the number of vibrissae present. The ulnar carpal group is the most interesting

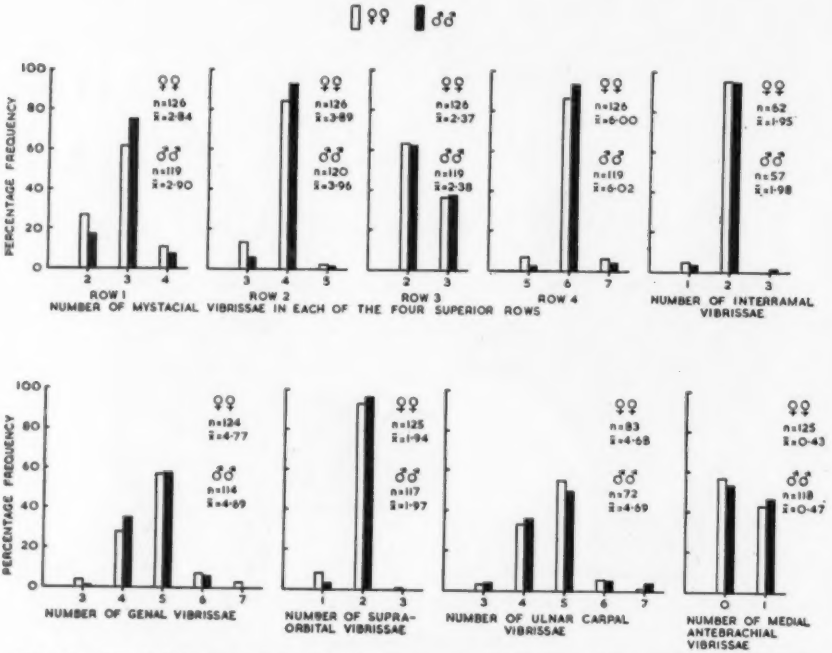


Fig. 12.—*Pseudocheirus convolutor* (Oken). Frequency distribution of the number of vibrissae in males and females. n=number of rows or groups of vibrissae examined. $\bar{x}$=mean number of vibrissae. Submental, calcaneal and lower rows of mystacial vibrissae not included.

as it is only in this group that the male shows a distinct tendency to develop more vibrissae than does the female.

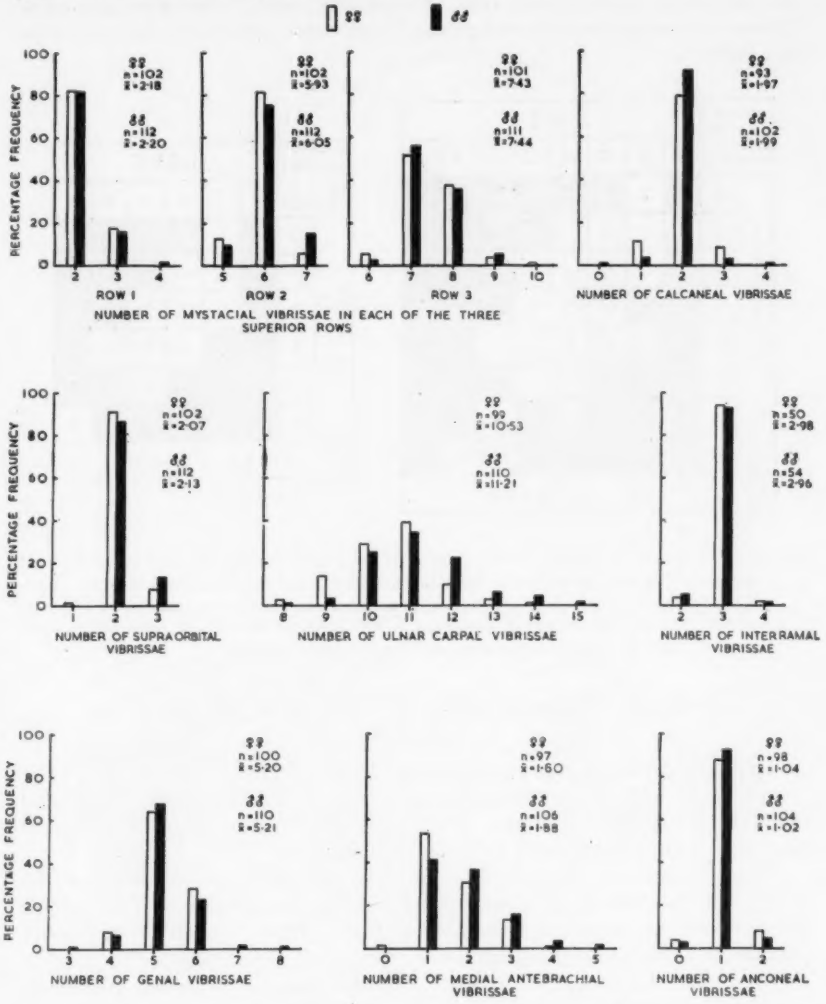


Fig. 13.—*Trichosurus vulpecula* (Kerr). Frequency distribution of the number of vibrissae in males and females. n=number of rows or groups of vibrissae examined. $\bar{x}$=mean number of vibrissae. Submental and lower rows of mystacial vibrissae not included.

In *T. vulpecula* the number of specimens showing bilateral symmetry and asymmetry in vibrissa number in two forearm groups is shown diagrammatically in Fig. 14. P_1=the percentage of specimens showing bilateral symmetry

in vibrissa number in a row or group. P_2=the percentage of specimens in which the number of vibrissae on the right and left sides of a row or group does not differ by more than one. Values of P_1 and P_2 for other groups of vibrissae in this species and some groups in other marsupials are referred to later (see Table 7).

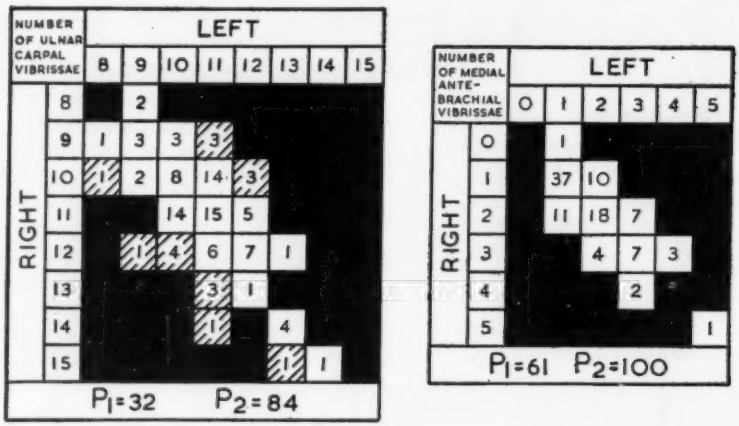


Fig. 14.—*Trichosurus vulpecula* (Kerr). Number of specimens showing bilateral symmetry and asymmetry in vibrissa number in the ulnar carpal and medial antebrachial groups. P_1= the percentage of specimens showing bilateral symmetry in vibrissa number in a row or group. P_2=the percentage of specimens in which the number of vibrissae on the right and left sides of a row or group does not differ by more than one.

Family II. **Phascolarctidae** (Pl. 4, A and Fig. 15, A)

Material

1. *Phascolarctos cinereus* (Goldfuss). Koala.

Nat. Mus. Vict.—four female pouch-young. C.603 (H+B 200), no data ; R.11334 (H+B 163), Victoria. Two other specimens without registration numbers ; 1 (H+B 210) and 2 (H+B 270), no data.

The vibrissae of *Phascolarctos cinereus*, the only representative of the family Phascolarctidae, are poorly developed and the number of facial groups in the specimens examined is reduced to four. There is no trace of sensory papillae or vibrissae on the limbs.

The mystacial group is not very extensive and the vibrissae, like those elsewhere, are short and inconspicuous. Most of the mystacial vibrissae are placed near the upper lip and there is little or no arrangement in rows. No attempt was made to count the actual number of vibrissae in this group. A small genal papilla gives rise to from two to eight short vibrissae. The supraorbital papilla is the best developed. It is situated almost directly above the anterior canthus and gives rise to from three to eight vibrissae. Usually the supraorbital vibrissae are a little longer and stronger than the genals. No

attempt was made to count the numerous submentals (Fig. 15, A). The vibrissae of this group are short and mostly directed downwards and forwards. There is no trace of the interramal group and, as mentioned above, there are

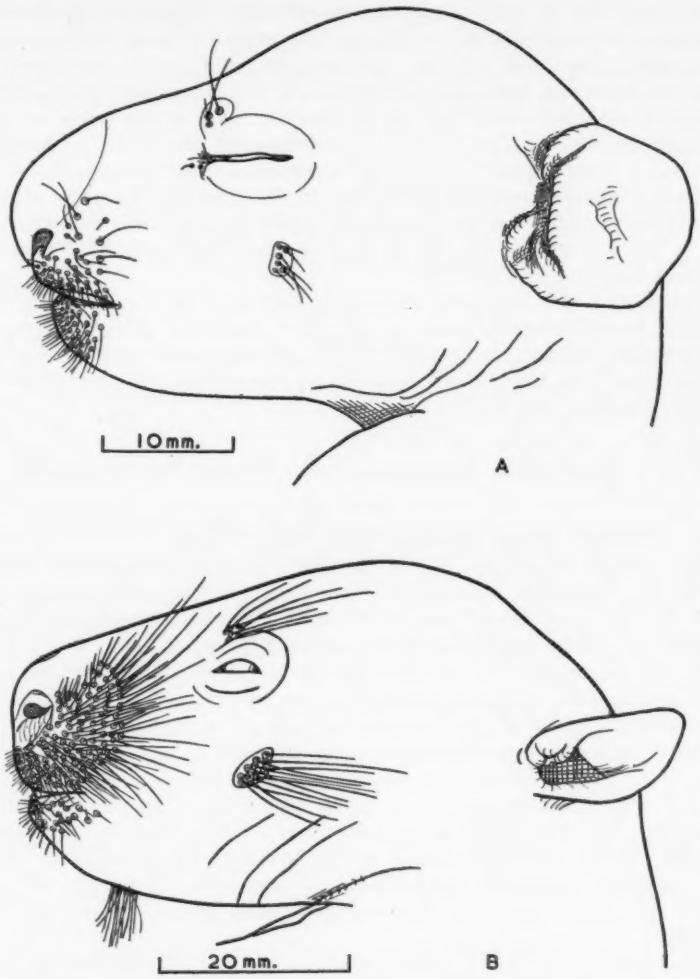


Fig. 15.—A, *Phascolarctos cinereus* (Goldfuss). Nat. Mus. Vict. C.603, female pouch-young. Facial vibrissae. B, *Vombatus ursinus* (Shaw). ×128, male pouch-young. Facial vibrissae.

no vibrissae on the limbs. In specimen C.603 (Fig. 15, A) there are several short vibrissa-like hairs immediately in front of the anterior canthus. These

hairs may represent the suborbital group found in *Wallabia rufogrisea* (Desmarest) and in various other macropods.

The vibrissae of *P. cinereus* have been described by Pocock (1921), Wood Jones (1923a) and Boardman (1943). Wood Jones, in a single specimen, found three only of the five typical sets of facial vibrissae. Pocock figures the head of an adult animal and showed four groups of facial vibrissae and he commented that "the vibrissae are comparatively poorly developed, the mystacial especially, being few and short and the interramal tuft wanting". Boardman also said that "one of the characteristics of the adult animal is the poor development of the sensory vibrissae of the head". Boardman examined a series of pouch-young and he remarked that "As growth proceeds the genal papillae become less prominent; in the oldest specimen the vibrissae are still recognizable but the associated papilla is more easily palpated than seen". Of the interramal and forearm groups, Boardman said that they were not observed at any stage.

Evidently Wood Jones considered only the upper portion of the mystacial group as he said that the group is reduced to about six short vibrissae. In the specimens used in the present study there are numerous small mystacial vibrissae near the margin of the upper lip, in addition to the larger more superior ones (see Fig. 15, A).

Family III. **Vombatidae** (Pl. 4, B and Fig. 15, B)

Material

1. *Vombatus ursinus* (Shaw). Tasmanian wombat.

Six juvenile specimens (H+B 180–315) from Tasmania and Flinders Island (see Table 5). Two specimens belong to the author's collection; specimens nine and twenty-two are in the Tas. Mus., and specimens four and 277a are in the Zoological Society of London's Prosectorium.

In all specimens the full complement of vibrissae has erupted. The distribution of the vibrissae (excluding the mystacials and submentals) in the specimens examined is shown in Table 5. The mystacial group is very extensive and its numerous vibrissae are arranged in many ill-defined rows (Fig. 15, B). No attempt was made to count the vibrissae of this large group. On the chin there are numerous short submental vibrissae not regularly arranged. The ulnar carpal group may or may not be represented (see Table 5).

Wood Jones (1924a) in a single female pouch-young of *Vombatus ursinus* from Tasmania found five supraorbital vibrissae, seven genals, and two ulnar carpals on each side. The unpaired interramal group had about twelve vibrissae.

Boardman (1943) from a number of specimens of *Vombatus hirsutus* (Perry) recorded that the genal papilla gives rise to nine or ten vibrissae. He did not mention the number of interramals and ulnar carpals.

The most notable feature presented by this investigation of six specimens of *Vombatus ursinus* is the wide range of variation in the number of vibrissae present in the different groups (see Table 5). One possible explanation for this numerical variability is that the groups of vibrissae are in the process

of being lost. This is evident in the two specimens without trace of the ulnar carpal group. In another specimen there is a solitary unilateral ulnar carpal vibrissa. In the remainder there are two to five ulnar carpal vibrissae. The same range of variation is seen in the various facial groups, shown in Table 5, but some vibrissae always remain in each group.

TABLE 5

Vombatus ursinus (Shaw). Distribution of the vibrissae (except the mystacials and submentals) in six juvenile specimens from Tasmania and Flinders Island

Specimen and sex	Genal		Supraorbital		Inter-ramal	Ulnar carpal	
	R	L	R	L		R	L
×128 (Tas.) ♂	13	12	7	7	14	3	2
×129 (Tas.) ♂	9	11	7	6	13	0	1
9 (F.I.) ♂	11	11	8	8	8	4	4
22 (Tas.) ♀	11	11	8	9	17	0	0
4 (F.I.) ♂	8	7	6	7	13	0	0
277a (Tas.) ♀	12	12	10	9	—	5	5

Family IV. **Macropodidae** (Pl. 5, and Figs. 16–19)

Material

1. *Bettongia gaimardi* (Desmarest). Gaimard's rat-kangaroo.

Two female pouch-young—1 (H+B 110) and 2 (H+B 160) from New South Wales. Specimens in Embryology Dept., University College, London (Professor J. P. Hill collection).

2. *Bettongia cuniculus* (Ogilby). Tasmanian rat-kangaroo.

Fourteen pouch-young (H+B 68–165) and one adult (H+B 410) from Tasmania ; three specimens in Prosectorium, Zoological Society, London ; six specimens in author's collection ; remainder in Tas. Mus.

3. *Potorous tridactylus* (Kerr). Dark rat-kangaroo.

Fifteen pouch-young (H+B 69–175) from Tasmania and one adult (H+B 335) from Victoria ; two specimens in Prosectorium, Zoological Society, London ; three specimens in author's collection ; nine specimens in Tas. Mus., and remainder in Nat. Mus. Vict.

4. *Caloprymnus campestris* (Gould). Desert rat-kangaroo.

Three specimens from Mulka, via Marree, South Australia ; C.241, adult male (H+B 335) ; R.13609, adult female (H+B 300) ; R.13610, female (H+B 255).

5. *Dendrolagus bennettianus* De Vis. Bennett's tree-kangaroo.

Nat. Mus. Vict., 55992, female pouch-young (H+B 210) from North Queensland.

6. *Dendrolagus inustus* Schlegel and Müller. Brown tree-kangaroo.

M.6214, juvenile female (H+B 286) from Eitape, Sepik Division, New Guinea.

7. *Lagorchestes hirsutus* Gould. Western hare-wallaby.

R.13122, juvenile female (H+B 210) from 80 miles north of Chearing's Well, Northern Territory.

8. *Petrogale lateralis* Gould. Black-flanked rock-wallaby.

R.12532, female pouch-young (H+B 213) from Macdonnell Ranges, Central Australia.

9. *Setonix brachyurus* (Quoy and Gaimard). Quokka.

X750, male pouch-young (H+B 100) from Perth, Western Australia.

10. *Thylogale billardierii* (Desmarest). Tasmanian rufus-bellied wallaby.

Twenty-six pouch-young (H+B 80–200), twelve females and fourteen males from Tasmania ; nine specimens in author's collection : the remainder in Tas. Mus.

11. *Wallabia rufogrisea* (Desmarest). Bennett's wallaby.

Forty-two pouch-young—thirteen females and twenty-seven males from Tasmania and two males from Flinders Island. Nine specimens in author's collection : remainder in Tas. Mus.

12. *Macropus tasmaniensis* (Le Souef). Tasmanian forester kangaroo.

X365, adult (head only ; length 215 mm.) from Gladstone, Tasmania.

A summary of the distribution of the vibrissae in the Macropodidae examined is shown in Table 6. All the typical facial groups of vibrissae are represented, except in *Caloprymnus campestris* (Fig. 17) and *Dendrolagus bennettianus* which are without interramals. In addition to the typical facial vibrissae, two other groups, the suborbital (Fig. 18, A) or rhinal (Figs. 18, B and 19, A), or both (Fig. 19, B), are present in most of the Macropodinae examined.

The principal mystacial vibrissae are usually arranged in four or five rows but they may be irregularly arranged. In addition, there are a number of smaller vibrissae near the margin of the upper lip. In *Wallabia rufogrisea* and *Macropus tasmaniensis* (Table 6) the mystacial vibrissae of the two upper rows are counted together.

As a rule the genal group is small (not more than five vibrissae) and the supraorbital group is well represented (Table 6).

A comparison of the distribution of most of the vibrissae in the two rat-kangaroos (*Bettongia cuniculus* and *Potorous tridactylus*) recorded from Tasmania is shown in Fig. 16.

The vibrissae of a number of representatives of the family Macropodidae have been previously described. Those of *Hypsiprymnodon moschatus* Ramsay have been recorded by Heighway (1939), who said that the facial vibrissae stand out from the general fur and referred to earlier observations by Owen (1879). Owen observed "a few scattered supralabial, malar, and superorbital vibrissae, black, fine in texture, about an inch in length". Heighway examined six specimens of *Hypsiprymnodon* and recorded that "In these specimens the supralabial (mystacial) to the number of twelve-fourteen on each

Distribution of the vibrissae in the Macropodidae*

Species and number of specimens examined	Mystacial			Genal	Supraorbital	Interramal	Ulnar carpal
	Row 1	Row 2	Row 3				
Bettongia gaimardi (Desmarest) (2)	2–3	3–4	6	2	3–5	2	1–4
Bettongia cuniculus (Ogilby) (15)	2	3	5–6	2	3–4	2	1–2
Potorous tridactylus (Kerr) (16)	1–2	4–5	5–6	1–2	2	1–2	1–4
Caloprymnus campestris (Gould) (3)	2–3	2–3	4	1	2–3	0	4–7
Dendrolagus bennettianus De Vis (1)	3	3	7	4	4–5	0	0
Dendrolagus inustus Müll. & Schleg. (1)	2–3	3	4	5	6	2	0–2
Lagorchestes hirsutus Gould (1)	1	2	4	3–4	3	2	2
Petrogale lateralis Gould (1)	2	3	6	3	6	2	2
Setonix brachyurus (Quoy & Gaimard) (1)	2	3	5	3–4	4	1	1–2
Thylogale billardierii (Desmarest) (26)	1	3–5	5–7	2–3	3–5	1–3	1–4
Wallabia rufogrisea (Desmarest) (42)	3–9		4–6	2–5	4–8	1–3	1–2
Macropus tasmaniensis (Le Souef) (1)	5		7	3	6	4	?

* Rhinal, suborbital, submental and lower mystacial vibrissae not included.

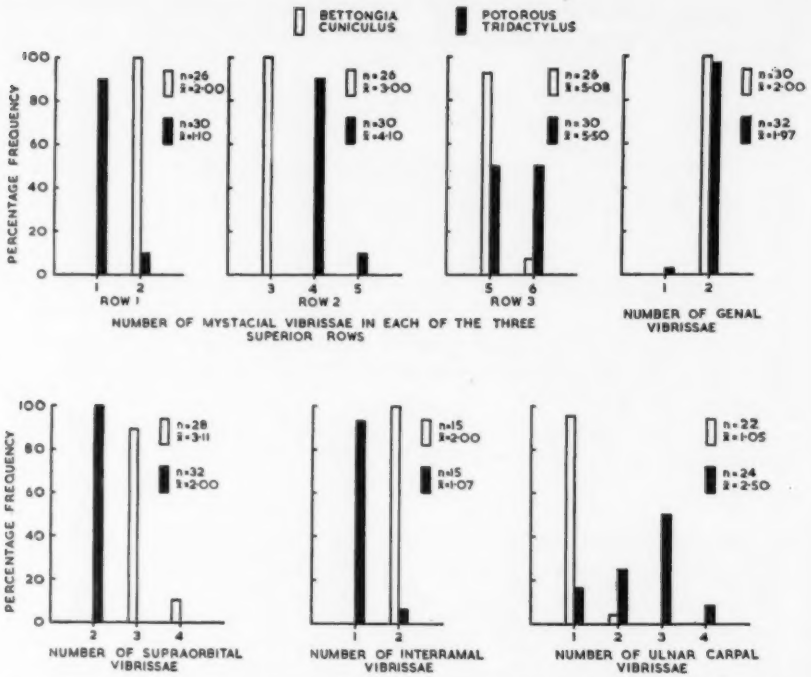


Fig. 16.—Frequency distribution of the number of vibrissae in *Bettongia cuniculus* (Ogilby) and *Potorous tridactylus* (Kerr). n=number of rows or groups of vibrissae examined. $\bar{x}$= mean number of vibrissae. Submental and lower rows of mystacial vibrissae not included.

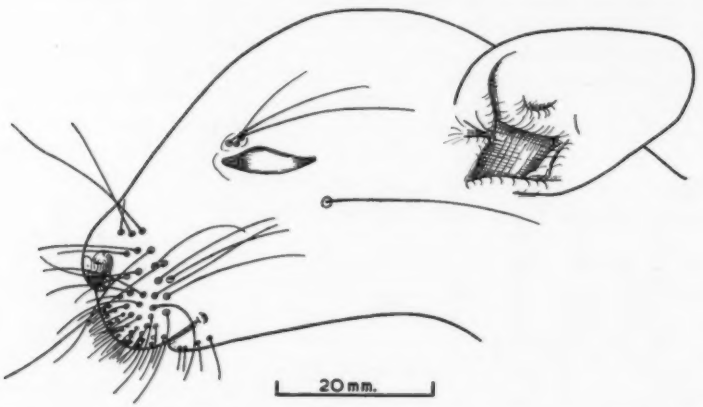


Fig. 17.—*Caloprymnus campestris* (Gould). Nat. Mus. Vict. R.13610, adult female. Facial vibrissae.

side, supraorbital (two on each side) and malar or genal (three on each side) were readily detected, some exceeding 25 mm. in length. In addition, a pair of interramal and an indefinite number of submental vibrissae could be demonstrated in every specimen examined. Anconeal (1) medial antebrachial (1) and ulnar carpal (2) vibrissae could generally be detected ; the ulnar carpal were the longest, some exceeding 30 mm. in length. Calcaneal vibrissae could not be found ". According to Heighway, Carlsson (1915) regarded the presence of carpal vibrissae as a link with the potoroos. As ulnar carpal vibrissae are common to most marsupials (see Fig. 20) this statement by Carlsson is of little value.

Pocock (1914, pp. 892–895) briefly described the facial vibrissae of *Aepyprymnus rufescens* Gray, *Thylogale billardierii*, *Wallabia rufogrisea*, *Petrogale penicillata* Griffith, Smith and Pidgeon, and *Dendrolagus ursinus* Schlegel and Müller. For *Aepyprymnus*, Pocock said that all the facial vibrissae are retained but are shorter than in two phalangers, *Trichosurus vulpecula* and *Pseudocheirus peregrinus* which he described in the same paper. According to Pocock, the genals of *Aepyprymnus* are situated " high up in a horizontal line with the base of the ear and only a little below the posterior canthus of the eye ". A figure of the head of *Aepyprymnus* shows three supraorbital, four genal, three interramal, three submental, and numerous mystacial vibrissae. For *Thylogale billardierii*, Pocock mentioned " only one genal bristle in the same position as in *Aepyprymnus*, and two short and fine interramals ". In the present study twenty-six specimens of *T. billardierii* (Fig. 19, A) have been examined but in no specimen does the genal set contain a solitary vibrissa only. The interramal group in *T. billardierii* is usually represented by a single vibrissa, occasionally two or three. In *Macropus bennettii* (= *Wallabia rufogrisea*), Pocock recorded one interramal vibrissa and a strong tuft of genals near the middle region of the cheek, below and behind the posterior canthus. Forty-two specimens of this species have been examined. In these specimens the interramal group is usually represented by a solitary vibrissa but two or three may be present. The genal group usually contains three or four vibrissae but two or five are occasionally found (Pl. 5, B and Fig. 19, B). In no specimen are the genals a strong tuft, although the group is better developed herein than in most macropods (see Table 6). For *Petrogale penicillata*, Pocock described "A pair of genals high up, in almost the same position as in *Aepyprymnus*. Interramals absent ". In an aged specimen of *Dendrolagus ursinus*, Pocock found that the vibrissae are reduced in number and length. There was a single genal vibrissa in nearly the same position as in *Aepyprymnus*, and the interramals were absent.

In the two species of *Dendrolagus* examined (see Table 6) the genal group consists of four or five vibrissae and the interramal group is represented by two vibrissae in one species and none in the other.

Garrod (1875, p. 51, Pl. 8) showed four large interramal vibrissa follicles in a specimen of *Dorcopsis luctuosus* (D'Albertis).

Wood Jones (1924 a) described the vibrissae of a juvenile specimen of *Dendrolagus matschiei*, Förster and Rothschild. The vibrissae were not particularly well developed. The supraorbital papilla gave rise to four

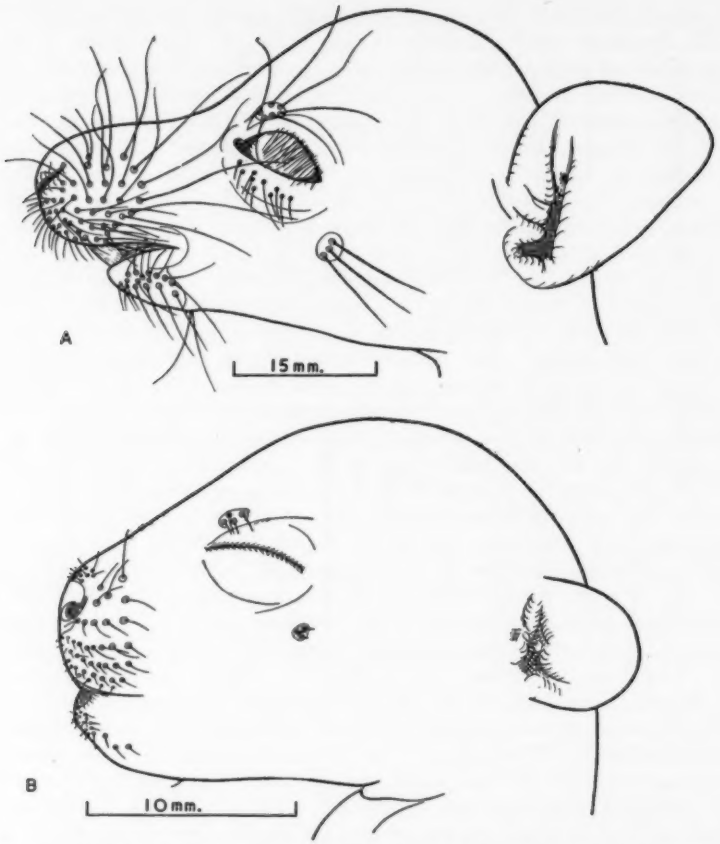


Fig. 18.—A, *Petrogale lateralis* Gould. Nat. Mus. Vict. R.12532, female pouch-young. Facial vibrissae. B, *Setonix brachyurus* (Quoy and Gaimard). ×750, male pouch-young. Facial vibrissae.

vibrissae. The genal papilla, which was partially subdivided into two papillae, gave rise to three vibrissae. The mystacial group was poorly developed. The interramal group was represented by two well-defined papillae, one on each side of the middle line, each bearing two vibrissae. The ulnar carpal group was represented by a solitary vibrissa.

In *Bettongia lesueuri* (Quoy and Gaimard) Wood Jones (1924 c) said "The facial vibrissae are fairly well developed, all sets being represented. The supraorbital vibrissae form a group of three or four, of which one is the longest (45 mm.) of all the facial bristles. The mysticial set is arranged in five rows, and the longest vibrissa is 35 mm. All the facial vibrissae are black. One white ulnar carpal vibrissa, 15 mm. long is recognisable in the adult".

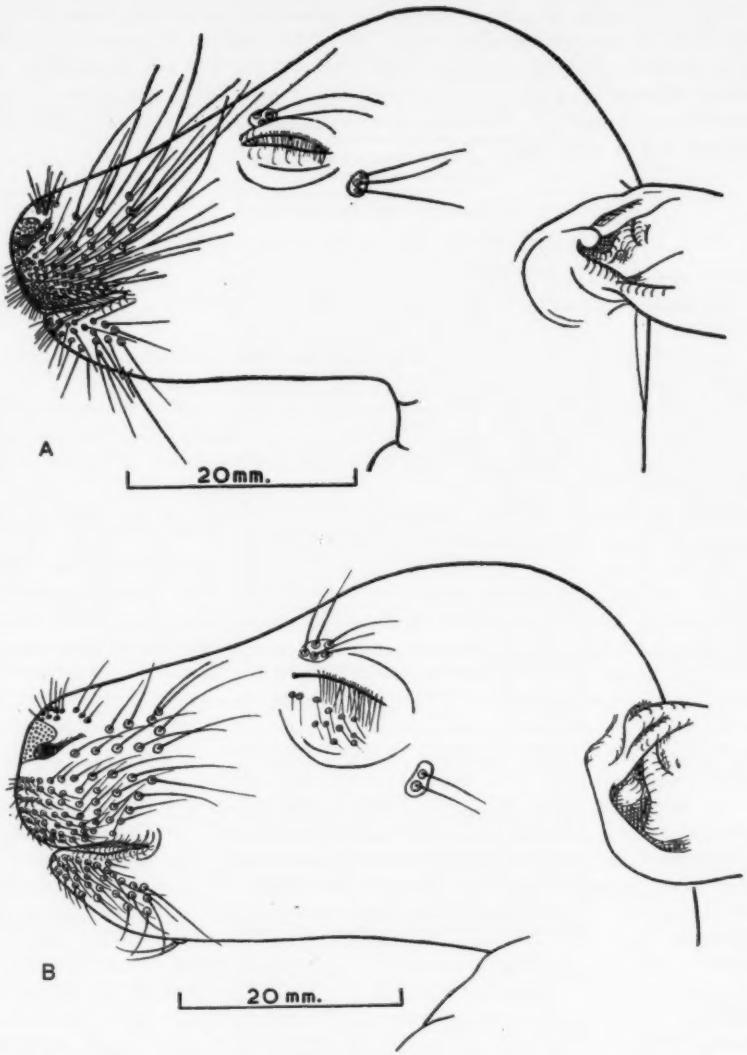


Fig. 19.—A, *Thylogale billardierii* (Desmarest). ×332, female pouch-young. Facial vibrissae. B, *Wallabia rufogrisea* (Desmarest). ×5, female pouch-young. Facial vibrissae.

Reference has already been made to Clarke (1948) who provides a description of the vibrissae in *Setonix brachyurus*. The facial vibrissae of a small pouch-young of this species are shown in Fig. 18, B.

Hypsiprymnodon is unique among the macropods in having three groups of brachial vibrissae (Heighway, 1939). In all the macropods examined in the course of the present investigation (see Table 6) there is one group only of forearm vibrissae, usually poorly developed, especially in the larger representatives of the family. In one species, *Dendrolagus bennettianus*, no forearm vibrissae can be detected.

DISCUSSION AND CONCLUSIONS

(a) *Special characters of the vibrissae of marsupials*

A summary of the distribution of the principal groups of vibrissae (excluding the rhinals and suborbitals) in all the marsupials examined is shown in Figs. 20 and 21.

In most marsupials the vibrissae are the first hairs to appear. *Trichosurus vulpecula* and several other marsupials are exceptional in that no vibrissae are visible until practically the whole of the skin is covered by a coat of hairs. Gibbs (1938) has already drawn attention to this unique character of hair formation in *Trichosurus* and suggested that it is probably associated with development in the pouch, characteristic of the marsupials. Gibbs was not, however, aware that very few marsupials show this early development of the first pelage hairs.

The sequence of appearance of the vibrissae is not described in detail herein. At birth, however, no vibrissae or pelage hairs project above the skin surface. *Perameles gunnii* is an example of a typical marsupial in which the vibrissae erupt before the pelage hairs ; in this species representatives of the mystacial, genal, supraorbital and ulnar carpal groups erupt before the interramals and submentals. Within the mystacial group the vibrissae placed at the posterior ends of the rows are the first to appear. The sequence of eruption of the vibrissae is found to be constant within each of the other species examined.

All the marsupials examined (except the highly specialized *Notorcytes typhlops*) possess vibrissae, which are usually arranged upon a definite plan. On the head, the mystacial and genal vibrissae are always present : the latter group is single except in *Tarsipes spenserae*, where two groups may be represented (Fig. 9). The supraorbital group is absent in but one species (*Acrobates pygmaeus*) and the submental group is also wanting on one species (*Macrotis lagotis*). Of the typical facial groups of vibrissae, the most commonly reduced or absent is the interramal group (see Fig. 20). The absence of interramal vibrissae is a character common to the Caenolestidae, Phascolarctidae and Phalangeridae (except *Pseudocheirus convolutor* and *Trichosurus vulpecula* and sometimes *Tarsipes spenserae* and *Schoinobates volans*). In addition, this group is absent in several peramelids and in two macropods. Suborbital and/or rhinal vibrissae (not shown in Fig. 20) are usually present in the Macropodinae but have not been recorded in other marsupials.

There may be as many as three separate groups of forearm vibrissae. The ulnar carpal group is present in all marsupials examined except *Thylacinus cynocephalus*, *Phascolarctos cinereus* and *Dendrolagus bennettianus*. In several

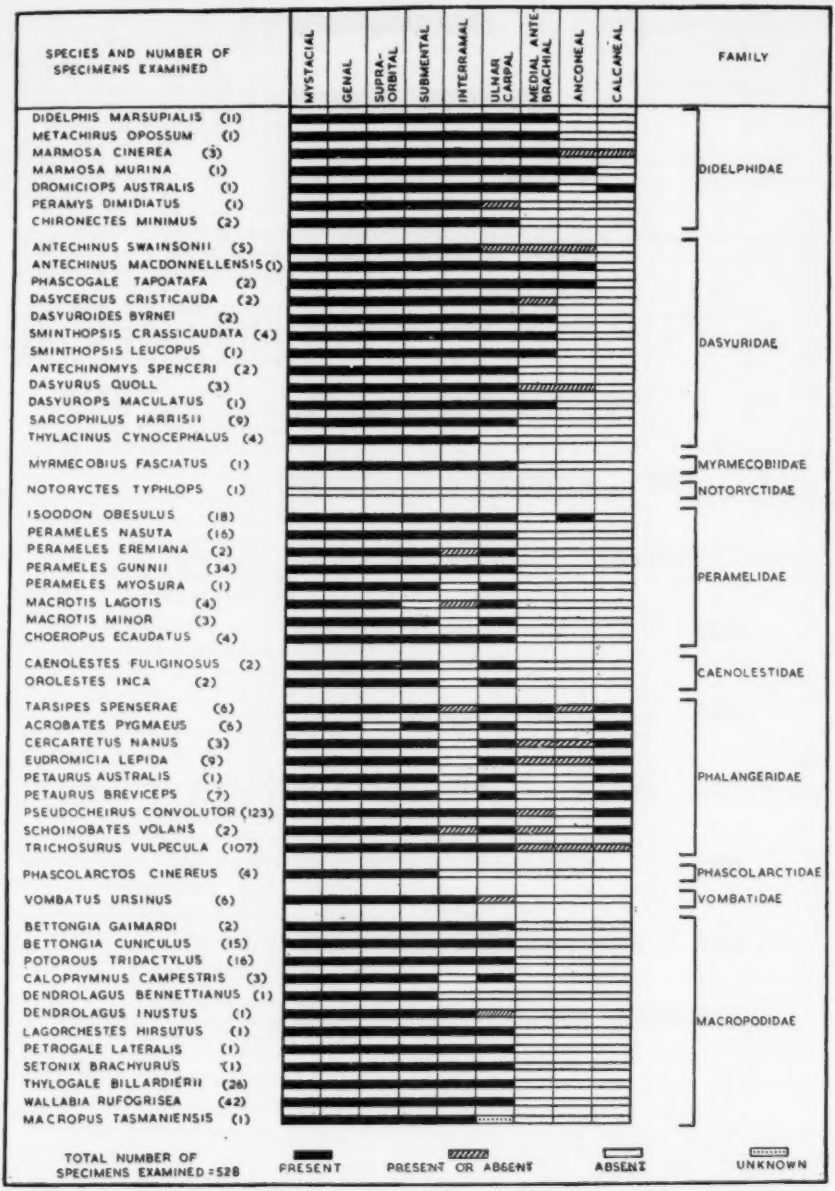


Fig. 20.—Summary of the distribution of the principal groups of vibrissae in all the marsupials examined. It has not been possible to examine a forearm of *Macropus tasmaniensis*.

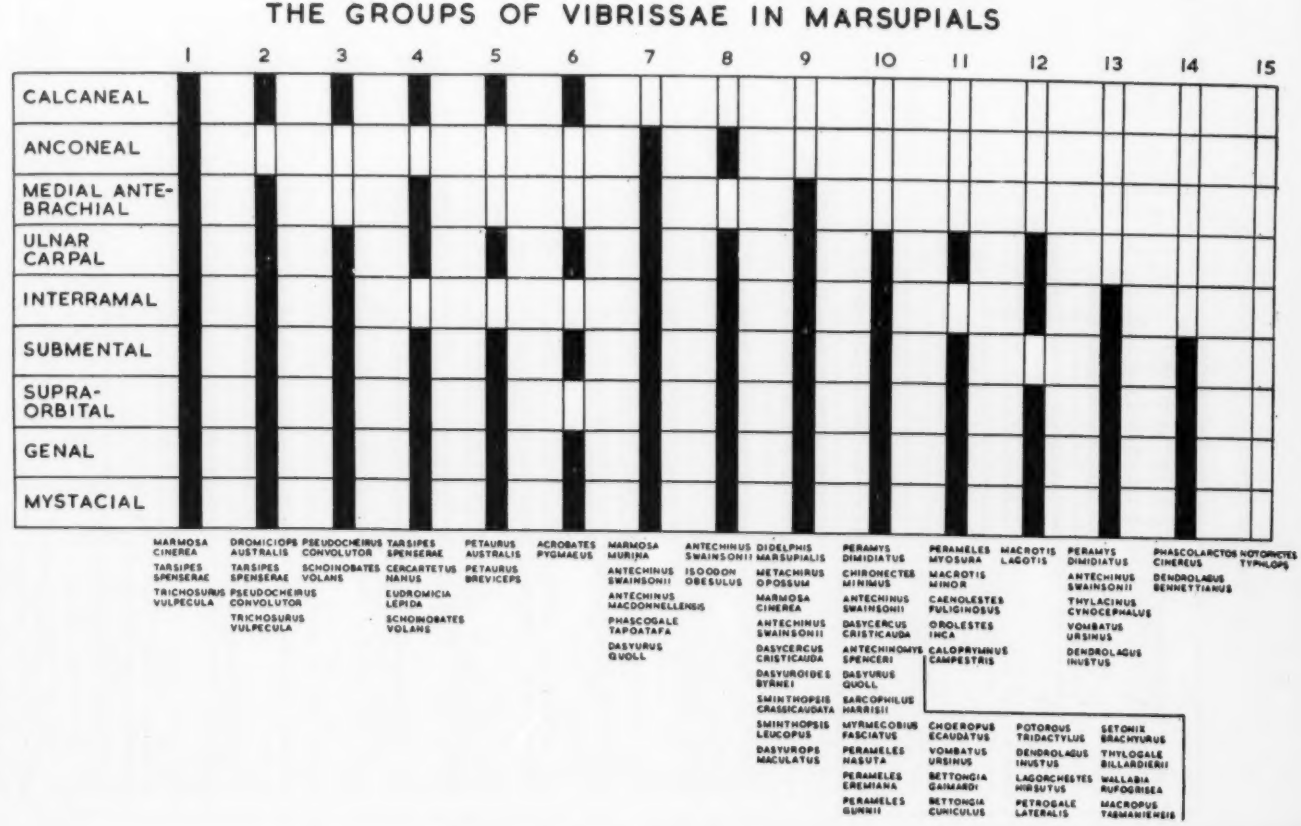


Fig. 21.—Arrangement of the marsupials examined according to the distribution of their principal vibrissae. The first category includes those species which may possess all the principal groups of vibrissae. For other details see text.

other species (see Fig. 20) the ulnar carpal group is present in some individuals and absent in others. Medial antebrachial and/or anconeal vibrissae are present in most of the arboreal marsupials, as well as in the genera *Isoodon* and *Hypsiprymnodon*. The vibrissae of the latter genus have been described by Heighway (1939).

On the hind-limb the calcaneal group of vibrissae is represented in all the phalangers as well as in several arboreal didelphids (see Fig. 20). In other marsupials no calcaneal vibrissae can be detected.

With the exception of the interramal group, the vibrissae are all in paired groups and, for any one individual, the number in each of the two groups is practically identical. The number of vibrissae present in each group may, or may not, vary slightly among the different individuals of a species.

The vibrissae of some groups show a remarkable numerical constancy between animals of the same or even of different species or different families. For example, in the Didelphidae, Peramelidae and Phalangeridae, there are, with few exceptions, two supraorbital vibrissae. Other examples of the numerical constancy of the vibrissae of one or more groups are found in most of the marsupials examined. Occasionally, as in *Vombatus ursinus*, the number of vibrissae present in each group may vary considerably (see Table 5).

In order to simplify a comparison of three facial groups, the genal, supraorbital and interramal, the mean number of vibrissae in each group has been determined for each species examined. The genal vibrissae (Fig. 22) are most numerous in the Dasyuridae and least numerous in the Macropodidae. The supraorbital vibrissae (Fig. 23) are most numerous in the Phascolarctidae, Vombatidae and Macropodidae and in several highly specialized dasyurids. The vibrissae of this group, as mentioned above, show a remarkable numerical constancy in many of the marsupials examined. The unpaired interramal group (Fig. 24) is well developed in the Didelphidae, Dasyuridae and Vombatidae, poorly developed in the Phalangeridae and absent in the Caenolestidae and Phascolarctidae. For other details see Fig. 24.

For comparison, the various marsupials examined have also been arranged according to the distribution of their vibrissae (see Fig. 21). (Two facial groups of vibrissae, the rhinal and suborbital, found only in the Macropodinae, are not included in this comparison). Fifteen categories are shown in Fig. 21. The first category includes all the marsupials examined which may possess all the typical groups of vibrissae. Only three of the fifty-four species fall into this category. Those species which may possess all the typical groups of vibrissae except the anconeals fall into the second category. The first six categories include only those marsupials which possess calcaneal vibrissae. The representatives are all arboreal species and they include all the Phalangeridae as well as two Didelphidae. For other details see Fig. 21.

Within each family (see Fig. 20) the species which have fewer groups of vibrissae are the more specialized types, whereas those which have all or most groups present are the more generalized types. This may be seen by comparing : in the Dasyuridae, *Antechinus* with *Thylacinus*, the former being a primitive, and the latter a highly specialized dasyurid ; in the Peramelidae,

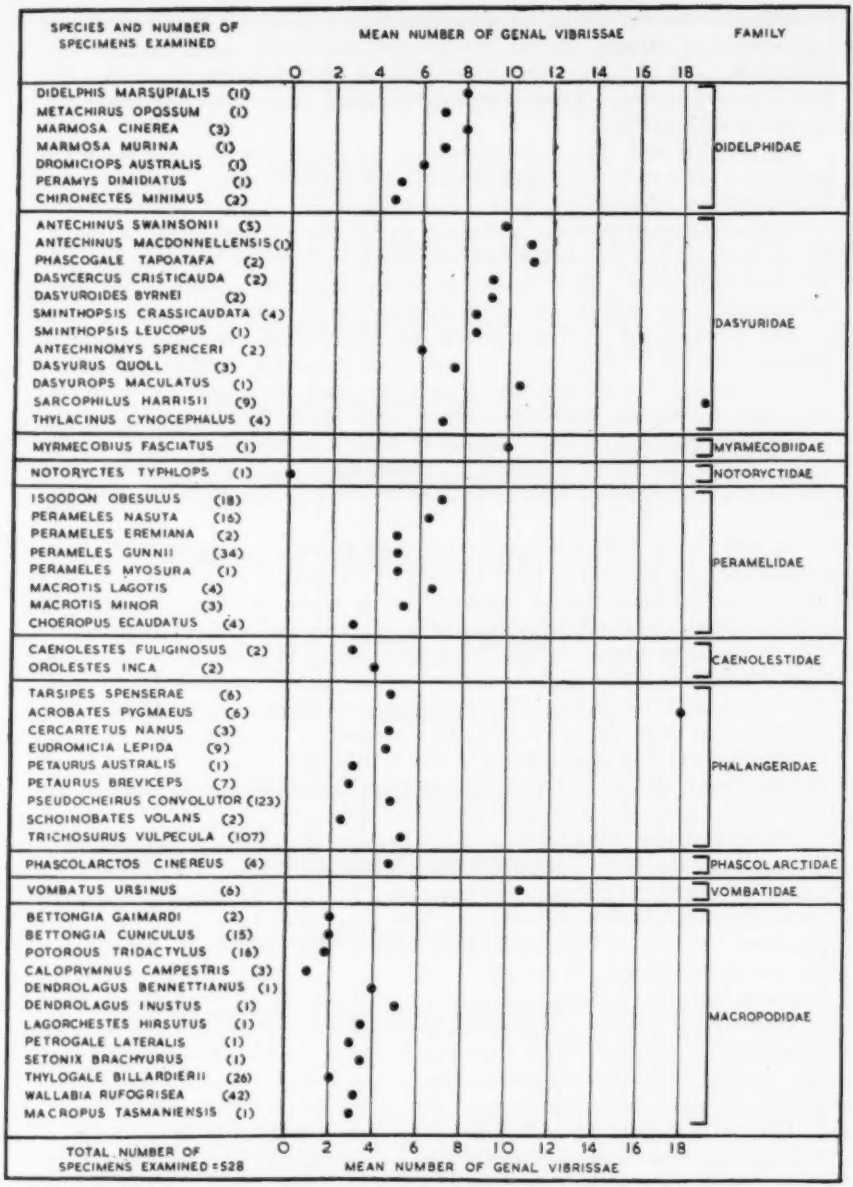


Fig. 22.—Mean number of genal vibrissae in the marsupials examined. Note that the vibrissae of this group are most numerous in the Dasyuridae and least numerous in the Macropodidae.

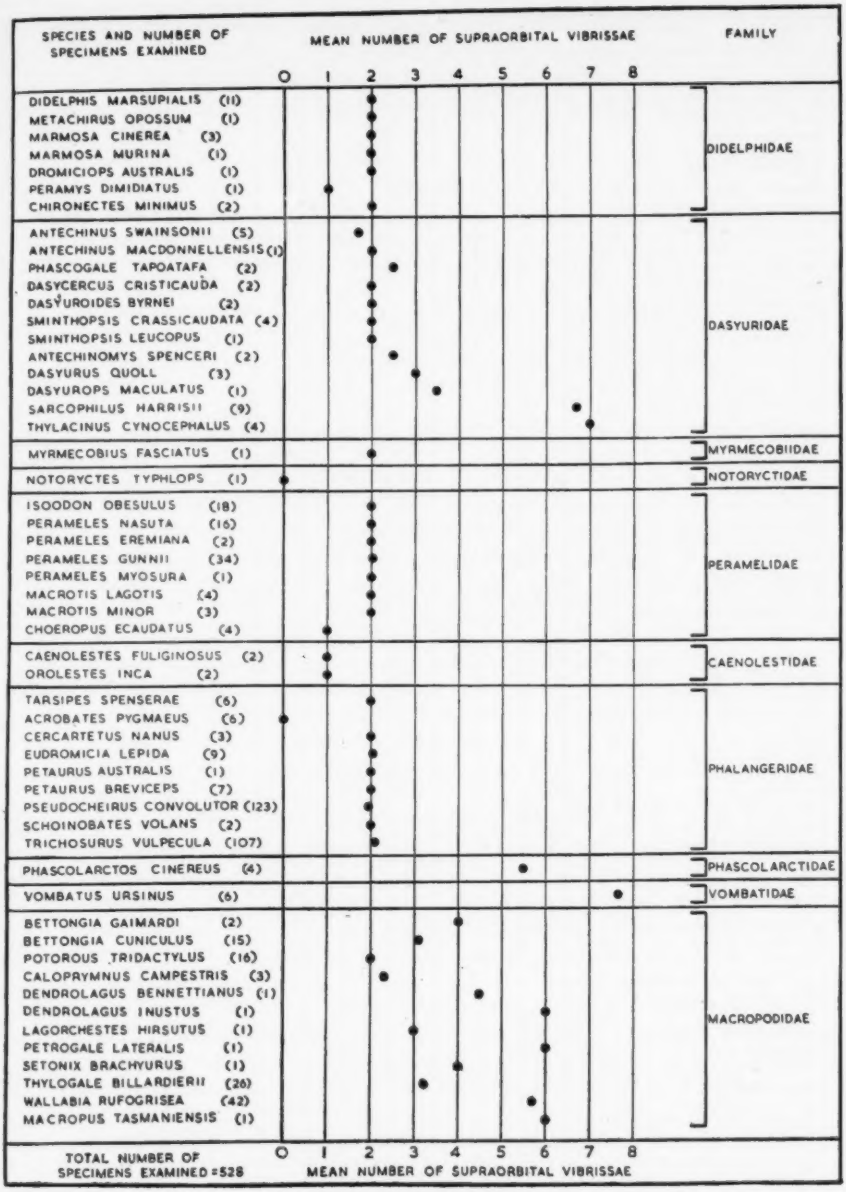


Fig. 23.—Mean number of supraorbital vibrissae in the marsupials examined. Note that this number is remarkably constant within and between certain families.

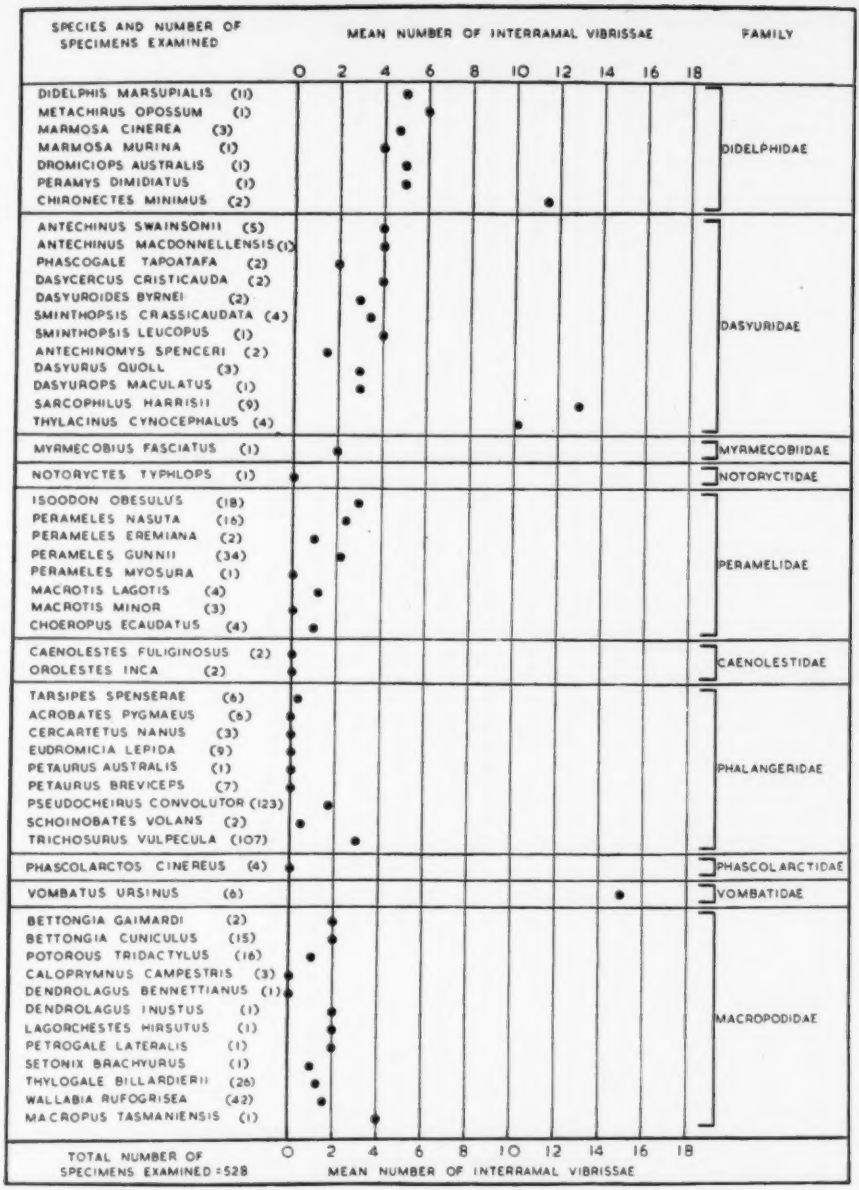


Fig. 24.—Mean number of interramal vibrissae in the marsupials examined. Note that this group is poorly developed in the Phalangeridae and absent in the Caenolestidae and Phascolarctidae.

Isoodon with *Choeropus* ; in the Phalangeridae, *Trichosurus* with *Acrobates* ; and in the Macropodidae, *Hypsiprymnodon* with *Dendrolagus*.

In agreement with the findings of Pocock (1914) and Wood Jones (1929) it is concluded that a full set of vibrissae is to be considered as a primitive characteristic.

The observations recorded here suggest that the vibrissae are intimately related to mode of life (Fig. 25). Attention is drawn to the following features of the vibrissae :—

(a) Complete absence in the subterranean marsupial mole, *Notoryctes typhlops*.

(b) Deficiency (particularly of mystacial and submental vibrissae) in the ant-eater, *Myrmecobius fasciatus*.

(c) High degree of development in the active arboreal genera, *Marmosa*, *Tarsipes*, *Trichosurus* and others.

(d) Reduction in the slow climbing genera, *Phascolarctos* and *Dendrolagus*.

(e) Reduction or complete absence on the limbs in those genera which do not use their limbs for grasping and in those genera which have well developed hind-limbs ; for example, in *Thylacinus* and various macropods. The reduction in the number of ulnar carpals is probably related to the lack of facilities for their use.

Usually, there is no discernible sex difference in the number of vibrissae present in the various species examined. A large number of specimens of two species, *Pseudocheirus convolutor* and *Trichosurus vulpecula*, have been examined in an endeavour to find out whether their vibrissae show any sex difference. In *Trichosurus* (Fig. 13) the most interesting groups are the ulnar carpals and medial antebrachials. The mean number of ulnar carpal vibrissae is 11·2 in males and 10·5 in females. Although not great this difference in number is highly significant. For the medial antebrachial group the difference is less (1·9 in males and 1·6 in females) but it is just significant. In *Pseudocheirus* (Fig. 12), and in the other species examined, no significant sex differences in the number of vibrissae can be detected.

The degree of symmetry in vibrissa number has been investigated in a number of the marsupials examined. In one species, *Trichosurus vulpecula*, the number of specimens showing bilateral symmetry and asymmetry in vibrissa number in two groups is shown diagrammatically in Fig. 14. Values of P_1 and P_2 (for definitions see Fig. 14) in some of the marsupials examined are shown in Table 7. The number of vibrissae present in each paired row or group is more likely to be the same than different. When the number is different the extra vibrissa or vibrissae may be on either side of the body. The value of P_1 decreases as the size of the row or group increases (Fig. 26). When the mean number of vibrissae in a row or group is four or less, the value of P_1 is more than fifty. However, when the mean number is more than four the value of P_1 may be less than fifty. When the mean number is more than ten, the value of P_1 is not greater than fifty. The value of P_2 is seldom less than seventy-five (see Table 7).

Geographically isolated representatives of a species show little or no difference in the distribution of their vibrissae. For example, the vibrissae of a Central Australian *Isoodon obesulus* are similar to those of specimens collected in Tasmania. Also, the vibrissae of a specimen of *Trichosurus vulpecula* from Perth, Western Australia, are similar to those of Tasmanian specimens.

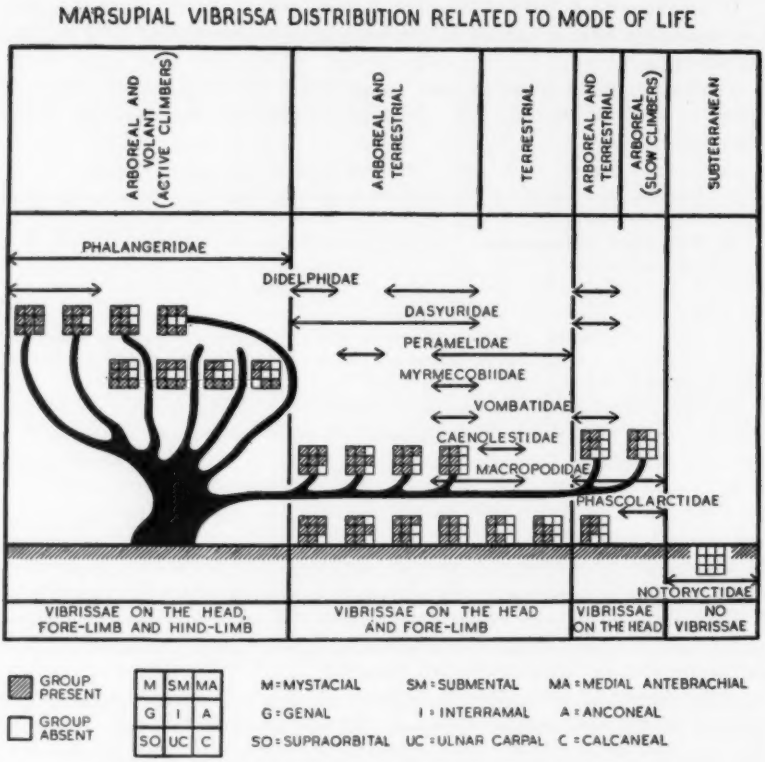


Fig. 25.—Marsupial vibrissa distribution related to mode of life. Each large square represents the distribution in some or all members of the families indicated (species are shown in Fig. 21). It is divided into nine small squares each representing a vibrissa group as shown in the key. When the group is present the small square is hatched. The animals in the first column, with vibrissae on the head, fore-limb and hind-limb, are all active climbers and some are volant. All the Phalangeridae and two of the Didelphidae examined are represented here. The animals in the next column, which have vibrissae on the head and fore-limb, are arboreal and terrestrial or terrestrial only. Members of seven out of the ten families with living representatives are in this column. Of the animals in the next column, with vibrissae on the head only, some are arboreal and terrestrial and some are arboreal but only slow climbers, for example, the koala and tree-kangaroos. In the last column is one animal, the subterranean marsupial mole, with no vibrissae.

TABLE 7

Degree of symmetry in vibrissa number in some of the marsupials examined

Species and number of specimens examined	Mystacial						Genal	Supra-orbital	Sub-mental	Ulnar carpal	Medial ante-brachial	Anconeal	Calcaneal
	Row 1	Row 2	Row 3	Row 4	Row 5	Row 6							
	P_1 P_2	P_1 P_2	P_1 P_2	P_1 P_2	P_1 P_2	P_1 P_2	P_1 P_2	P_1 P_2	P_1 P_2	P_1 P_2	P_1 P_2	P_1 P_2	P_1 P_2
Didelphis marsupialis (11)	100 100	100 100	100 100	78 100	? ?	? ?	56 100	100 100	75 100	25 75	78 100	0 0	0 0
Sarcophilus harrisii (9)	71 100	67 100	67 100	100 100	? ?	? ?	43 71	71 100	? ?	20 40	0 0	0 0	0 0
Thylacinus cynocephalus (4)	100 100	100 100	100 100	100 100	25 100	50 100	50 75	50 100	50 75	0 0	0 0	0 0	0 0
Isoodon obesulus (18)	83 100	100 100	94 100	78 100	71 94	88 100	100 100	100 100	81 100	94 100	0 0	100 100	0 0
Perameles nasuta (16)	93 100	100 100	100 100	75 100	27 87	81 94	81 100	100 100	75 100	100 100	0 0	0 0	0 0
Perameles gunnii (34)	94 100	97 100	94 100	88 100	23 87	81 100	94 100	100 100	70 100	100 100	0 0	0 0	0 0
Pseudocheirus convolutor (123)	73 100	93 100	61 100	88 100	? ?	? ?	66 99	94 100	? ?	52 94	93 100	0 0	? ?
Trichosurus vulpecula (107)	87 100	78 99	70 100	? ?	? ?	? ?	75 96	94 100	? ?	32 84	61 100	82 100	89 100
Vombatus ursinus (6)	? ?	? ?	? ?	? ?	? ?	? ?	50 83	33 100	? ?	67 100	0 0	0 0	0 0
Bettongia cuniculus (15)	100 100	100 100	85 100	? ?	? ?	? ?	100 100	79 100	? ?	90 100	0 0	0 0	0 0
Thylogale billardierii (26)	100 100	92 100	60 100	? ?	? ?	? ?	77 100	81 100	? ?	81 100	0 0	0 0	0 0

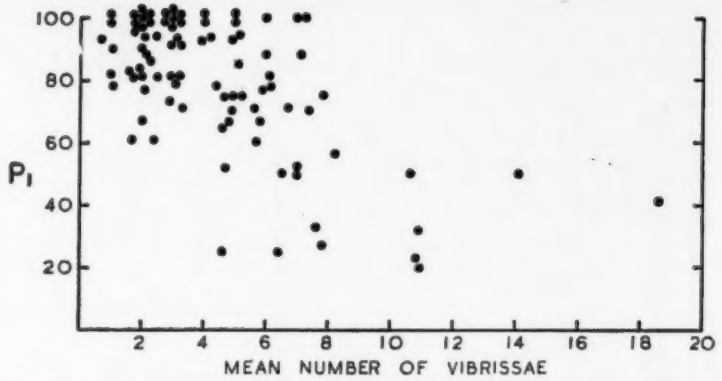


Fig. 26.—Values of P_1, shown in Table 7, plotted against the mean number of vibrissae. Note that the value of P_1 decreases as the size of the row or group increases. For definition of P_1 see Fig. 14.

(b) *Characters of the marsupial vibrissae in relation to monotremes and placental mammals*

Few authors, other than Beddard (1902) and Pocock (1914), have attempted a general survey of the distribution of the vibrissae in the various orders of mammals. Unfortunately, there is insufficient information in the literature to make more than a few brief comparisons of the vibrissae of marsupials with those of other mammals. However, the conclusions of Pocock and Beddard are in close agreement with those derived from the present investigation of a large number of marsupials.

The marsupial mole, *Notoryctes*, resembles the monotremes, *Tachyglossus* and *Ornithorhynchus*, in lacking vibrissae. Pocock (1914) suggested that the vibrissae of monotremes have been lost. In the marsupial ant-eater, *Myrmecobius*, the mystacial and submental vibrissae are greatly reduced and the fore-limb vibrissae, represented by a single group, are poorly developed. Pocock (1914) examined several edentate ant-eaters and recorded vibrissae as absent, as in *Tachyglossus*, or but poorly developed.

The active arboreal marsupials resemble placental mammals of a similar mode of life, such as squirrels, in having well developed vibrissae. The slow climbers, like *Phascolarctos* and *Dendrolagus* among the marsupials, resemble slow climbers like *Bradypus* among the Edentata, and *Perodicticus* among the Primates, in having poorly developed vibrissae (Pocock, 1914). In reference to the Primates Pocock remarked that "The deterioration of the vibrissae passing upwards from the lowly organised lemurs to the more highly organised monkeys and apes is probably correlated with the gradual perfection of the hands, carrying with it increased sensitiveness of touch".

Beddard (1902) examined the ulnar carpal vibrissae of various mammals (including a number of marsupials) and remarked that these vibrissae must

be of some use to their possessors, though such use is not easy to demonstrate. Earlier Beddard (1900) recorded the presence of similar vibrissae in a variety of mammals (including Lemuroidea, Carnivora, Rodentia and Marsupialia) and remarked that he " invariably found these structures in those members of the groups in question which use their forepaws as climbing or grasping organs, or in both ways ".

The present investigations confirm Beddard's observations in respect to the marsupials. Although ulnar carpal vibrissae are present in most marsupials, medial antebrachial and/or anconeal vibrissae are present, with few exceptions, in arboreal species only. Calcaneal vibrissae, present in some active arboreal marsupials, have not been recorded in placental mammals.

SUMMARY

1. The distribution of vibrissae is described and illustrated in representatives of all the families of marsupials. A total of 528 specimens from fifty-four species has been examined : these include nine species from South America and forty-five species from Australasia, including nineteen of the twenty living species recorded from Tasmania. The vibrissae in each species have been examined, and a summary, including notes on literature, is given for each family.

2. Vibrissae are present in all the marsupials examined, except *Notoryctes typhlops*, and they are arranged upon a definite plan.

3. The sequence of eruption of the vibrissae is constant within a species, and, with few exceptions, vibrissae appear before pelage hairs.

4. On the head :

(a) Mystacial and genal vibrissae are always present.

(b) Supraorbital vibrissae are present in all species except *Acrobates pygmaeus*.

(c) Submental vibrissae are present in all species except *Macrotis lagotis*.

(d) The interramal group is the most commonly reduced or absent. The absence of interramals is a characteristic of the Caenolestidae, Phascolarctidae and most of the Phalangeridae. In addition, the interramals are absent in several Peramelidae and Macropodidae.

(e) Suborbital and/or rhinal vibrissae are present in only one family, the Macropodidae.

5. On the limbs :

(a) Ulnar carpal vibrissae are present in all the marsupials examined except *Thylacinus cynocephalus*, *Phascolarctos cinereus* and *Dendrolagus bennettianus*. In several other species ulnar carpal vibrissae are present in some individuals and absent in others.

(b) Medial antebrachial and/or anconeal vibrissae are present in most of the arboreal marsupials, as well as in the terrestrial genera *Isoodon* and *Hypsiprymnodon*.

(c) Calcaneal vibrissae are present in all the Phalangeridae and two of the Didelphidae examined.

6. There is a remarkable numerical constancy of vibrissae in some of the groups between animals of the same species or even of different species or different families : e.g., in the Didelphidae, Peramelidae and Phalangeridae, there are, with few exceptions, two supraorbital vibrissae.

7. The number of vibrissae present within each group may be constant for members of a species (e.g., *Bettongia cuniculus*) or may vary considerably (e.g., *Vombatus ursinus*).

8. Usually, there is bilateral symmetry in a species with respect to the number of vibrissae present in a row or group. When the distribution is asymmetrical the extra vibrissa or vibrissae may be on either side of the body.

9. Usually, there is no sex difference in the number of vibrissae present in a species.

10. Geographically isolated representatives of a species show little or no difference in the distribution of their vibrissae.

11. The presence or absence of various groups of vibrissae (particularly on the limbs) and their degree of development tend to be alike in each family. However, within each family, species with fewer groups of vibrissae are the more specialized types, whereas, those with all (or most) groups present are the more generalized types.

12. From this (11), and in agreement with the findings of Pocock and Wood Jones, it is concluded that a full set of vibrissae is a primitive marsupial characteristic.

13. The distribution of the vibrissae is directly related to the mode of life of the species, as exemplified by :—

(a) their absence in *Notoryctes typhlops*,

(b) their deficiency in *Myrmecobius fasciatus*,

(c) their high degree of development in active arboreal genera,

(d) their reduction in slow climbing genera, and by

(e) their reduction on the fore-limbs of the Macropodidae.

14. A brief comparison of marsupials with other mammals reveals that mammalian vibrissae have a number of features in common. For example, the deficiency or complete absence of vibrissae in monotreme, marsupial and some placental ant-eaters, and the high degree of development of vibrissae in many active arboreal mammals.

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EXPLANATION OF THE PLATES

PLATE 1

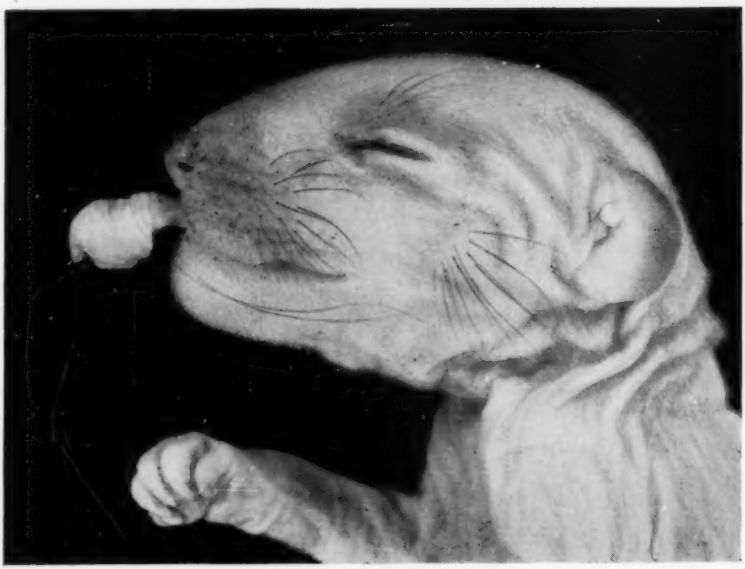
Fig. A.—*Metachirus opossum* (Linnaeus). A4. 11/3, juvenile male.

„ B.—*Sarcophilus harrisii* (Boitard). Tas. Mus. 586 B, female pouch-young.

PLATE 2

Acrobates pygmaeus (Shaw). R.8174, adult female.

A



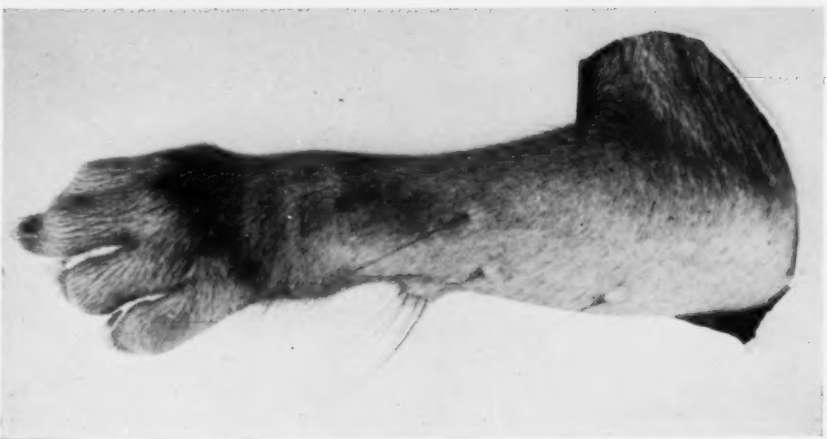
B

Fig. A.—*Metachirus opossum* (Linnæus) A 4. 11/3, juvenile male.

Fig. B.—*Sarcophilus harrisii* (Boitard) Tas. Mus. 586 B, female pouch—young.

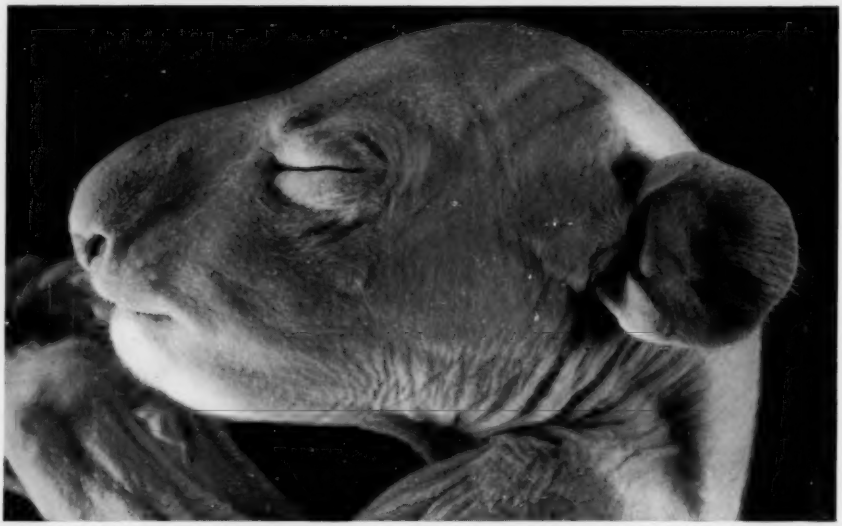
Acrobates pygmaeus (Shaw) R.8174, adult female.

A



B

Trichosurus vulpecula (Kerr)
A—Male pouch—young, × 51; B—Male pouch—young. Lateral view of forearm showing distribution of vibrissæ, × 86.



A

B

Fig. A.—*Phascolarctos cinereus* (Goldfuss) C.603, female pouch—young.
Fig. B.—*Vombatus ursinus* (Shaw) Female pouch—young, × 129.

A

B

Fig. A.—*Potorous tridactylus* (Kerr) Female pouch—young, × 136.

Fig. B.—*Wallabia rufogrisea* (Desmarest) Female pouch—young, × 5.

PLATE 3

Trichosurus vulpecula (Kerr)

Fig. A.—Male pouch-young. ×51.

„ B.—Male pouch-young. Lateral view of left forearm showing distribution of vibrissae. ×86.

PLATE 4

Fig. A.—*Phascolarctos cinereus* (Goldfuss). C.603, female pouch-young.

„ B.—*Vombatus ursinus* (Shaw). Female pouch-young. ×129.

PLATE 5

Fig. A.—*Potorous tridactylus* (Kerr). Female pouch-young. ×136.

„ B.—*Wallabia rufogrisea* (Desmarest). Female pouch-young. ×5.

THREE UNUSUAL RORQUAL WHALES FROM THE ANTARCTIC

BY

GORDON R. WILLIAMSON

8, *Woodside Avenue, Walton on Thames, Surrey*

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(With 2 plates and 2 figures in the text)

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INTRODUCTION

Recently the "Balaena" Antarctic whaling expedition captured three small rorqual whales, i.e. *Balaenoptera* sp., which clearly differed in certain respects from any of the recognised species. A pregnant female was captured in 1955 and two males in 1957. All were of similar appearance and close to 27 feet in length. The two males were examined by the author in a very fresh condition on the deck of the factory ship, but the female is known only from photographs and some notes made at the time of capture. The whales closely resembled the minke whale, *Balaenoptera acutorostrata* Lacépède, 1804, but in contrast to this species the dorsal surface of the flipper was pale grey and showed no trace of the white band characteristic of *B. acutorostrata*. Furthermore the baleen of the latter species is uniform yellowish-white in colour, whereas the baleen of the three whales taken by "Balaena" was white at the front of the series and grey and white at the back.

It has been thought worth while to describe and discuss the specimens in some detail, and it is hoped that this paper may lead to further investigation of the matter.

The description is unfortunately based only on external characters because the whales had been worked up—in which process the bones are completely destroyed—before the author realised the significance of the peculiar colouration of the animals.

Details of the three whales are given in Table 1, and some measurements of whales 2 and 3 are listed in Table 2.

TABLE 1

Details of the three whales

	No. 1	No. 2	No. 3
Sex and length	♀ 27′ 0″	♂ 27′ 6″	♂ 26′ 11″
Position	62° S, 50° E	61° S, 50° E	58° S, 03° W
Date of capture	21. xii. 1955	28. xi. 1957	27. xii. 1957
Weight	7 metric tons	6¼ metric tons	
Foetus	4′ long		

No. 1 was pregnant with a 4 feet long foetus. The ovaries contained one corpus luteum but no corpora albicantia.

No. 2 had the stomach full of krill of large size, and some patches of diatoms were present on the skin. The testes weighed 1·55 and 1·77 kg.

No. 3 had the stomach full of very small krill and no diatom film was present. The belly blubber was 4 cms. thick.

TABLE 2

Measurements of whales 2 and 3

	No. 2 male captured 28. xi. 1957			No. 3 male captured 27. xii. 1957		
	feet	metres	% of total length	feet	metres	% of total length
Total length from snout to notch in flukes	27′ 6″	8·40	100	26′ 11″	8·20	100
Snout—middle of blowhole				3′ 10″	1·17	14·3
Snout—eye				4′ 10″	1·48	18·0
Snout—anterior insertion of flipper				7′ 8″	2·33	28·5
Snout—ant. edge of dorsal fin				17′ 7″	5·37	65·3
Vertical height of dorsal fin	1′ 11″	0·33	3·9	1′ 1″	0·33	3·9
Tip of mandible—penis				18′ 0″	5·50	67·0
Length of penis	2′ 0″	0·60	7·2	2′ 2″	0·66	8·0
Anus-notch in flukes				7′ 9″	2·37	28·9
Length of flipper from insertion to tip along leading edge				4′ 0″	1·22	14·8
Tail span	7′ 6″	2·29	27·4	6′ 10″	2·09	25·4
Maximum girth-about one yard behind the flippers				17′ 0″	5·20	63·5

DESCRIPTION OF THE WHALES

1. *The head, body and tail*

The whales are of typical slender rorqual shape (Fig. 1). The body is grey dorsally and white ventrally while laterally the two shades merge gradually together. A downward extension of dark pigment from the dorsal surface is

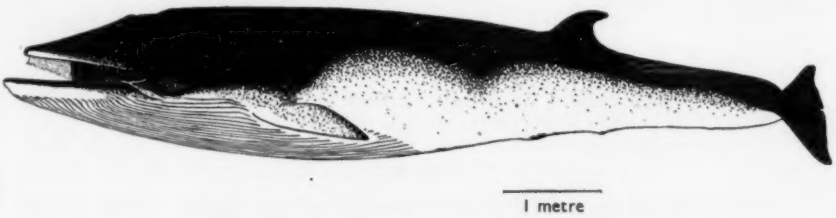

Fig. 1.—One of the whales taken by " Balaena ".

noticeable a short way anterior to the dorsal fin. The dorsal fin itself is large, strongly concave posteriorly, and of the same grey colour as the back of the animal (Fig. 1). It is a prominent feature of the living animal in the water.

The mandible is grey above, but white at the sides and below. The maxilla is mainly grey but the edges adjacent to the white section of the baleen are coloured white (Fig. 1), and in this respect closely resemble the condition in a fin whale, *B. physalus*. Altogether the animals look very like small fin whales, lacking only the extreme asymmetric colouration of the jaws and baleen.

The tail dorsally is pale grey, but along the thicker leading edges and along the mid line, the colour is somewhat darker (Fig. 2). Ventrally the tail is

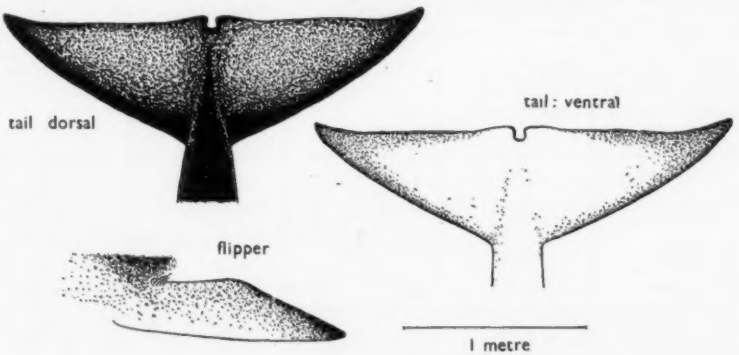

Fig. 2.—The tail and flipper of one of the " Balaena " whales.

white except for a grey border formed by extension of the dorsal pigmentation over the edge of the flukes. A notable feature of the tail is its almost triangular shape, which is due to the fact that the anterior and posterior borders are remarkably straight. The notch between the flukes is of variable form and not distinctive.

The ventral grooves are well developed as in all rorquals, and extend from the mandible to a point anterior to the umbilicus. In whale No. 2, a 27 feet 6 inches male, the grooves ended at a point about 30 cms. anterior to the umbilicus. When counted level with the flipper the grooves are about sixty-two in number.

2. *The flippers*

The general impression is that the flippers are of a pale grey colour dorsally (Fig. 2). In fact the leading edge is white, and the trailing edge darker, but the various shades merge imperceptibly into each other. The ventral surface is similar, though paler. On neither surface is there any trace of the white band which is characteristic of the flipper of *B. acutorostrata*. (Pl. 1, fig. 1).

3. *The baleen*

This is one of the most distinctive features of the whales. When viewed laterally the series is seen to consist of two parts : an anterior section of white plates followed by a sharply demarcated section of dark grey plates (Pl. 1, fig. 2). In fact the posterior plates are only dark grey along the outer edge and a large inner portion remains white in every plate right to the back of the series. The first plate that appears dark only has a very narrow dark border, but if one examines plates progressively nearer the back of the mouth the dark border will be seen to increase in breadth (Pl. 2, fig. 1). In whale No. 2, a 27 feet 6 inches male, the longest plate was 28 cms. long and had a dark grey band 4·0 cms. wide. A large portion of baleen was preserved from this whale and some measurements of these plates are recorded in Table 3.

TABLE 3

Details of the baleen of whale No. 2, a 27 feet 6 inches male.

Number of the plate counted from the anterior end of the series	Length of plate measured along outside edge	Lengths of hairs projecting from the end of the plate	Width of plate at a point 5 cm. from the gum	Width of the dark grey band
50th	12·0 cm.	5·5 cm.	2·5 cm.	no-band
75th	14·5	6·6	3·6	0·3 cm.
100th	17·5	5·5	6·0	2·5
150th	25·5	5·0	10·0	4·1
170th	28·0	6·0	12·0	4·0

Plates preserved : the anterior 172 from the left side.
Length of baleen series measured medianly: 1·56 metres.
Number of completely white plates: 75.
Estimated total number of plates in a complete side : 200.

From photographs and sections of baleen collected, correlated with measurements made on the carcases, it has been estimated that in whales 1 and 2 the number of plates originally present in each series was 200. This value is considerably lower than in *B. acutorostrata* (Table 4) or any of the other

well-known rorquals. In texture the baleen of the " Balaena " whales is very similar to that of *B. acutorostrata*, the hairs being neither as delicate as in a sei whale, nor as coarse as in Bryde's whale.

One interesting result of examination of photographs of whales 1 and 2 is that although the animals are of nearly the same length, the extent of the white baleen is variable. The variability is not only between individuals but, on occasion, between right and left sides of the same whale. This condition is not unprecedented, of course, for asymmetry and variation between individuals are well known in fin whales, *B. physalus*, and have also been noted in Bryde whales, *B. brydei*. The significance of the variations in the three whales taken by " Balaena " cannot be judged adequately until further material is available, but meanwhile the approximate extent of the variability is shown below :

Whale	Number of white plates (very approximate)	
	Right side	Left side
1	70	30
2	110	75

THE FOOD OF THE WHALES

The stomachs of whales 2 and 3 were filled with Antarctic krill, *Euphausia superba*. Whales No. 2, caught on 28th November 1957, in 61° S, 50° E., had been eating adult krill, the individuals being 5–6 cms. long. Whale No. 3 caught on 27th December 1957, in 58° S, 03° W, contained very small post-larval stages about 1·5 cms. long. Bull (1896) also reported " krill " from the stomach of a minke taken in the Antarctic. In the northern hemisphere the minke, *B. acutorostrata*, is more littoral in its distribution and often feeds on various species of small fish that occur in shoals near the coast, such as *Clupea* and *Mallotus* in Norway, and *Englaulis* and *Ammodytes* in Japan. Nevertheless the northern minkes appear to prefer euphausiids, for in areas where they are abundant the whales' stomachs contain much krill but no fish. In the Antarctic where krill is so abundant, and fish relatively scarce, it is not surprising to find the whales feeding on krill.

DISCUSSION

The small size of the whales, of which at least the pregnant female is adult, indicates that they cannot be specimens of any of the larger *Balaenoptera* species. The species they do resemble is the minke whale, *Balaenoptera acutorostrata*. This is a well-known whale that is hunted commercially in the northern hemisphere and has been extensively studied in Norway (Jonsgård, 1951) and Japan (Omura & Sakuira, 1956). It has also been seen in typical form in the southern hemisphere, but until recently it has seldom been taken and has not yet been studied there by biologists. In the northern hemisphere the species has been shown to have very constant external features, and these

differ considerably from those of the whales caught by " Balaena ", as described above. Though the baleen is usually uniformly yellowish in colour, Jonsgård (1951) has described specimens from Norway and the Arctic in which the plates each possess a narrow black border. However, these whales were quite normal in other respects, and I agree with Jonsgård in identifying them merely as slight variations of *B. acutorostrata*. The three whales taken by " Balaena " were somewhat longer than the average northern *B. acutorostrata*, but since it is well known that whales of the same species are larger in the southern oceans than in the north, this fact is not likely to be significant.

Apart from *B. acutorostrata*, two other species of small rorquals have been described, and they appear to resemble closely the three whales taken by " Balaena ". Both were described from single specimens, and they have remained little known because no further examples were ever found. *B. bonaerënsis* was described in 1867 by Burmeister from a dead male specimen found floating near Buenos Aires. The whale was large, approximately 32 feet long, and all the vertebral epiphyses were fused, which indicates that the animal was physically mature. It was dark grey dorsally and whitish ventrally, but the carcass was so decayed that the colour of the flipper could not be seen, and the animal was described as a new species on skeletal features. The majority of the left baleen series (192 plates) was recovered, and from this Burmeister estimated that the series had consisted of some 230 plates when complete. Each plate was coloured whitish on the inside but on the outer margin was black for a space of two inches. The original specimen is in the Buenos Aires public museum.

B. huttoni was described in 1874 by Gray from a young specimen found near Otago, New Zealand. The animal was 16 feet long and was described as a new species on skeletal features. The baleen plates were described as yellow with a narrow black margin, and were said to have a maximum length of 15 inches. However, Dr F. C. Fraser kindly gave me the opportunity to examine the specimen where it lies in the British Museum (Natural History), and I discovered that the original description was at fault in both respects. Though the more posterior plates possessed a black margin, the plates at the front of the series were plain (yellowish) in colour, as in the " Balaena " specimens. Unfortunately owing to age the baleen is now much warped and discoloured, and it was impossible to determine exactly how many plain plates existed at the front of the series. However it was possible to measure the breadth of the dark edge band, and on the longest plate which was 23 cms. (i.e. 5, not 15 inches) long, the band was 1·2 cm. broad. No mention was made of a white band on the flipper, but it is remarkable that this feature if it was present, was not shown on the sketch of the animal.

Several authorities have discussed the identity of *B. bonaërensis* and *B. huttoni* in the past, and all have recorded the opinion that the species are merely synonyms of *B. acutorostrata* (van Beneden & Gervais, 1880 ; Oliver, 1922). Flower (1885) records his opinion that *B. huttoni* is closely allied to, if not identical to *B. acutorostrata* while Jonsgård (1951) says that *B. bonaërensis* appears to be synonymous with *B. acutorostrata* from Norwegian waters, even with respect to the black borders present on the baleen plates.

In Table 4 the features of the various species are compared, and I think that the three whales caught by " Balaena " resemble *B. bonaërensis* and *B. huttoni* more closely than they resemble *B. acutorostrata*.

TABLE 4
Comparison of the small rorquals

	B. acutorostrata	The ' Balaena ' whales	*B. bonaërensis*	*B. huttoni*
Baleen colouration	yellowish white	white and dark grey	white with black border	yellowish with dark border
Flipper colouration	grey with white band	pale grey	—	—
No. of baleen plates in the series	270–348 average 304′ (1) 266–295 average 275 (2)	200 estimated	230 estimated	—
Longest plate, excluding bristles	23·5 cms. (1)	28 cms. in 27′ 6″ male	about 30 cms.	—
Distribution	cooler waters of N & S hemispheres	Antarctic	Argentina	New Zealand

(1) 99 specimens examined in Norway by Jonsgård (1951)

(2) 6 specimens examined in Japan by Omura & Sakiura (1956)

Many objections can be raised against erecting a new species for the " Balaena " whales. Thus in view of their great similarity to *B. bonaërensis*, and the likelihood that *B. huttoni* is also of the same species, it seems best to place all five specimens together under the name *B. bonaërensis*, since this takes precedence. No mention is made of a white front section of the baleen series in the original *B. bonaërensis* specimen, but in view of the brevity of the description, and the variability in the extent of the white baleen in the specimens caught by " Balaena ", it is not thought that too much weight can be placed on this point.

The existence of a new type of small rorqual, which for convenience we are calling *B. bonaërensis*, is admitted, but the question is still not solved as to whether it is a true and separate species, or whether it is a subspecies of *B. acutorostrata*. In this connection it is interesting to record some information about the distribution of the whales in the Antarctic.

All three specimens were taken near the pack ice between 58° S and 62° S, one at 03° W, the other two at 50° E. Considering the circumpolar uniformity of the Antarctic Ocean there is every reason to suppose that such whales would be found all around the Antarctic continent. Burmeister's record from Buenos Aires, and Gray's from New Zealand, indicate that the range extends north at least to 34° S. Unfortunately in most cases the parts of a whale underwater

cannot be perceived from a ship, and thus though whalers are familiar with small rorquals, all of which they call "minkes", the existence of two types has never been noted. The blow of a minke is almost invisible, and in rough weather the whales are seldom seen until they are very close to the ship. Then there is a flash of black back, and with what seems extraordinary speed they disappear beneath the surface. Only in calm weather can they be seen at any distance from the ship.

Some of the gunners of the " Balaena " expedition were kind enough to give me information about minkes which I now record, together with some data from other sources, but it must be remembered that the observations do not differentiate between *B. bonaërensis* and *B. acutorostrata*.

Minkes are plentiful all around the Antarctic Ocean and though common anywhere to the south of 50°S, the majority are found close to the edge of the pack ice. In fact they seem to prefer colder water than any other species and are often found in ponds in the pack ice. Taylor (1957) has a most interesting observation in this connection for, when watching a group of small rorquals in a pool in the fast ice off Grahamland, he could distinguish several whales with white patches on the flippers but also whales with them in which this feature could not be seen. Numbers of minkes are also found around South Georgia and Bouvet island, but the gunners have never seen minkes when whaling at Saldanha Bay (near Capetown), although strandings have occurred there. Generally minkes are seen in small groups of three or four, and I have seen many such groups myself, but sometimes they are very abundant in certain areas and are seen in " enormous flocks ". Mothers with calf are seldom seen. In the northern hemisphere *B. acutorostrata* performs an annual migration between the feeding grounds and warmer waters, and there is every reason to suppose that this also happens in the southern minke populations. It appears, however, that the minkes of the southern hemisphere do not migrate so far north in summer as the other rorqual species. If they did one would expect that they would be seen at Saldanha Bay with the other rorquals, for *B. acutorostrata* is a species known to frequent coastal waters. Strandings on the southern continents prove that minkes, do, on occasion, come further north, but whether these are regular visitors or merely stray whales cannot be determined. It is always possible that the southern minkes have different habits from their northern relations and migrate far from land where they are not seen.

Hitherto the value of the oil produced from such small whales hardly equalled the fuel expended in catching them, and in comparison with any of the larger whales a minke was worthless. Minkes in the Antarctic appear to have been taken first in the years 1894–95 when the whaling ship " Antarctic " killed two during a search for right whales. Since the hunting of rorquals in the southern oceans began in 1904, however, very few minkes have been taken, and these usually to provide fresh meat for the whalers. It is notable that in recent years the Soviet factory ship " Slava " has captured quite large numbers of minkes in the Antarctic, forty-one being taken 1955–56, forty-six in 1956–57 and 493 in 1957–58. There seems little doubt that minkes will be taken increasingly in future years as their value for frozen meat becomes appreciated and as the larger species of whale become scarcer.

CONCLUSIONS

B. bonaërensis appears to be unique amongst rorquals for it is apparently restricted to the southern hemisphere. Yet presumably it undertakes migrations each year like the other species. But if the new species evolved from *B. acutorostrata* stock why is it not found in the northern hemisphere? It must be emphasised, however, that our knowledge of *B. acutorostrata* in the southern oceans is only little better than our knowledge of *B. bonaërensis*, and despite the abundance of minkes scientific records are limited to a handful of strandings on the southern continents, and a few sightings at sea (Racovitza, 1903 ; Bull, 1896 ; Taylor, 1957).

Further information of all kinds is thus needed for both types of minke in the Antarctic, and owing to the great difficulty of distinguishing the two in the water the most fertile source will be the examination of dead whales on factory ships. Records to show the skeletal and colour variations in the two types, and their relative abundance, are specially needed, and until such information is available the problem cannot be finally solved. Meanwhile we can only admit that true identity of the *B. bonaërensis* whales is uncertain.

SUMMARY

Recently the "Balaena" Antarctic whaling expedition caught three small rorquals which differed in certain respects from the well-known minke whale, *B. acutorostrata*. Notably the colouration of the flippers and the baleen were unusual, for the flippers were plain grey while the baleen was white anteriorly and grey and white posteriorly.

The three whales bear striking resemblance to two little-known rorqual species that were described last century from single specimens found stranded on the southern continents ; *B. bonaërensis* at Buenos Aires and *B. huttoni* at Otago, New Zealand. In view of the close similarity of the five specimens it is suggested that they are all provisionally grouped together and considered as examples of the species, *B. bonaërensis*.

The gunners of the catcher boats have given me valuable information about minkes in the Antarctic, and say that they are found in all parallels of the Antarctic Ocean, and are particularly abundant close to the pack-ice. However it is almost impossible to distinguish the new type of minke from the normal *B. acutorostrata* while in the water, and thus all records are bound to refer to both types indiscriminately.

Small rorquals are abundant in the Antarctic but have seldom been taken owing to their very small value relative to the larger species.

Until further information is available concerning the features, and relative abundance of the two types of minke in the Antarctic, it is impossible to decide whether the five whales grouped as *B. bonaërensis* are a true and separate species, or whether they represent some subspecies of *B. acutorostrata*. If they are related to *B. acutorostrata* it is strange that they have never been recorded from the northern hemisphere.

ACKNOWLEDGMENTS

In connection with my biological work on " Balaena " I would like to thank two groups of people; firstly the many kind folk, British and Norwegian, who made the voyage so enjoyable, and secondly the people who have specially helped to produce this paper. The groups overlap considerably and as a start I would offer my sincere thanks for hospitality to the Hector Whaling Company, to Captain Virik and the crew of " Balaena ", to the senior whaling inspector Commander Henry Buckle, and to the ship's chemists. The after plan foreman Mr Westrum, and my two flenser friends Sigur and Trygre, often helped me on deck, for which I thank them. I am also indebted to Gunner Finn Ellefsen and his crew for their kind hospitality while on board the catcher Setter I.

The gunners of the fleet, notably Messrs Ellefsen, Krogtorp, Hem and Jensen gave me much information about the occurrence of minkes for which I am very grateful, and my thanks are also due to Mr Hugh Symons for some data about whale No. 1.

In England Dr N. A. Mackintosh and the National Institute of Oceanography kindly provided facilities to write this paper and, although the conclusions reached are my own, I am especially grateful to Mr Sidney Brown of the N.I.O. whose generous help has been invaluable in the writing of this paper.

Finally for the excellent photographs I thank Mr Christopher Ash and Mr Noel Baker, both of " Balaena ", and Mr Madgwick of the N.I.O.

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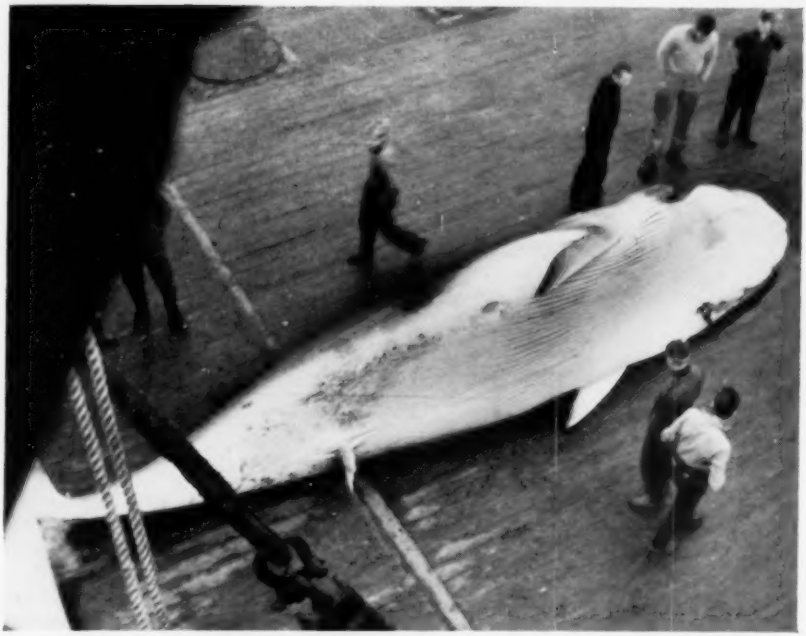

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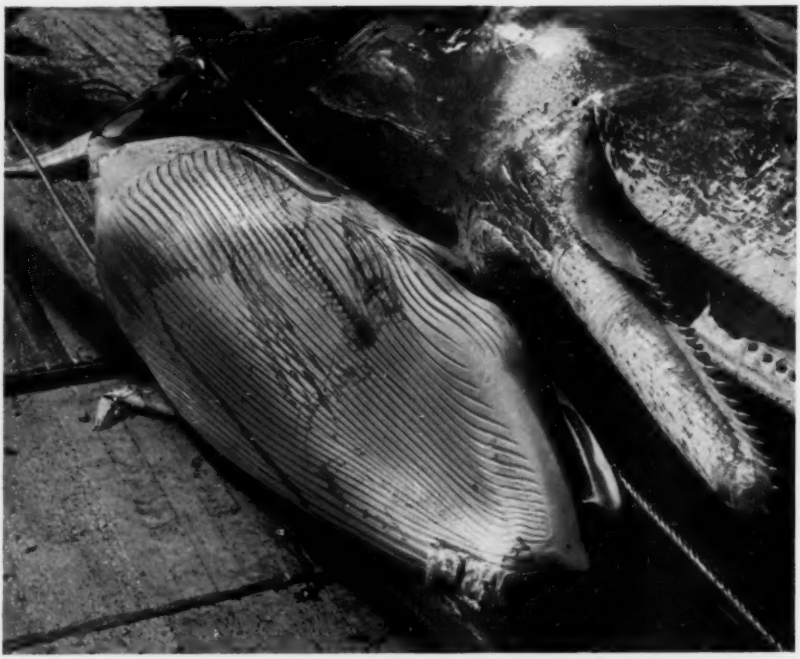
2

Fig. 1.—Whale No. 2 on the deck of the factory ship. Notice the coloration of the flipper. G.R.W.

Fig. 2.—The head of whale No. 2 showing the white anterior, and dark grey posterior portions of the baleen. N.B.

1



2

Fig. 1.—Baleen plates from whale No. 2 to show the development of the dark border along the series. The plates correspond approximately to Nos. 20, 65, 80, 110, 130, 170. N.I.O.

Fig. 2.—Whale No. 1 alongside a sperm whale *Physeter catodon*. C.A.

COURTSHIP AND MATING IN THE BUTHID SCORPIONS

BY

ANNE J. ALEXANDER

*Department of Zoology, Rhodes University, Grahamstown, South Africa**

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(With 7 figures in the text)

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INTRODUCTION

Both the earliest description of scorpion courtship (Maccary, 1810) and the classical one by Fabre (1923) deal with scorpions of the family Buthidae. Fabre never observed scorpions mating however. Recently Bücherl (1956) has given a description of the mating in the buthid genus *Tityus*, while a brief statement, added to a paper on scorpionid courtship and mating (Alexander, 1957), reported that mating in *Parabuthus planicauda* Poc. is similar to that which had been reported in other scorpion families, namely that there is uptake of sperm from a spermatophore deposited on the substratum by the male, a phenomenon which had been reported for the Chactidae (Angermann, 1955), the Scorpionidae (Alexander, 1956) and the Bothriuridae (de Zolessi, 1956). The present paper presents the evidence on which this earlier statement was based, together with an analysis of the behaviour patterns found in the courtship and observations on the formation and method of functioning of the spermatophore. The report relates to two buthid species in particular, *Parabuthus planicauda* of South Africa and *Tityus trinitatis* Poc. of Trinidad. A third species, *Uroplectes triangulifer* Thor., also of South Africa, will be referred to briefly.

SEXUAL DIFFERENCES

No gross sexual dimorphism is present in *P. planicauda* although the tergites on the mesosoma are slightly narrower in the male and there are differences both in the number of pectinal teeth and the form of the base of the

*Present address—Zoological Laboratories, Downing Street, Cambridge.

pectine. The external genital organs of the two sexes are also distinctive. In *T. trinitatis* similar sexual differences occur in the genital region (Fig. 1) but, in addition, there are other externally visible differences. Not only is the male bigger and longer, with a narrower body and relatively longer and narrower

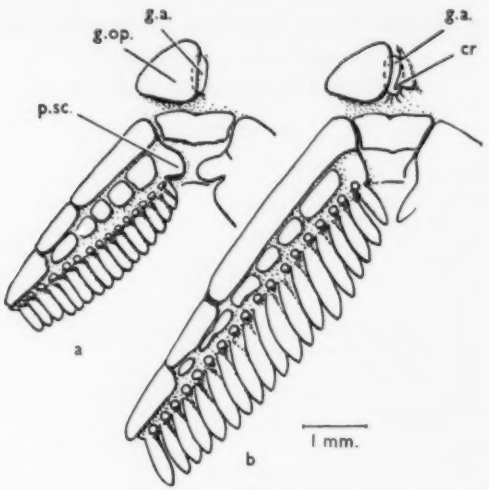

Fig. 1.—*Tityus trinitatis*, the pectinal region of (a) female and (b) male to show the sexual dimorphism. The male has more teeth in his pectine and these are longer than are those of the female. In each case the genital operculum, *g.op.*, has been cut away from the left side, exposing the genital aperture, *g.a.*, and, in the male, the crochet, *cr*. (see also Fig. 6b). At the base of the female pectine is a specialised lobe, *p. sc.*

tail, but even the colour is different. The female is purplish black all over, the male is chestnut with darker extremities, the contrasting colour being especially noticeable on the tail, the last two segments of which are black. The female retains the nymphal facies, while the male has a tail whose relative proportions and coloration are markedly different from those of last instar nymph.

INITIATION OF COURTSHIP

In *P. planicauda* there is no distinctive behaviour pattern associated with recognition of the sexes. It is clear however that a male can distinguish between the sexes for he will never court another male and, if two males approach each other closely, one will attack the other violently or run off rapidly. In an encounter of a male with a female, the two animals come close together before there is any indication of sexual recognition in their behaviour and indeed may be almost touching before any response occurs.

If the courtship proceeds, the male clutches at the female when they meet or as she passes him. The initial grasp may catch hold of any part of her body but the male gradually shifts his grip so that he comes to hold the female's two

pedipalps with his own. If she is not responsive, she will have escaped or beaten off the male with her tail before this. Occasionally a female who has been objecting to the advances of a male for some short time will suddenly allow him to take her pedipalps and proceed with the courtship. In such cases it is not clear whether she has been " stimulated " to this passivity or not.

In *T. trinitatis* the behaviour is slightly different in that the male grasps preferentially at the tail of the female : sometimes even when he already has hold of one of her pedipalps, he will relinquish it in favour of the tail-grasp. After tugging her about to a variable extent by the tail, the male gradually changes to the more conventional pedipalpar grasp. As with *P. planicauda*, the female *T. trinitatis* may object by pulling away and by beating the male with her tail. In both species the lance of the sting is tucked in, so that there is little possibility of the male being stung. Once the pedipalpar grasp is firmly established in either species, the pair is ready to being the " promenade à deux ".

PROMENADE A DEUX

During this the male drags the female about with him as he investigates the surface of the ground to find a site suitable for the deposition of a spermatophore. In the buthids the movements of this pattern are performed more rapidly than in the scorpionids. During the promenade, the male of *P. planicauda* normally uses one of his pedipalps to hold the female, so that he is facing the same way as he is leading the female. Just prior to the actual mating he does in fact return to the hold used earlier, that in which he holds both of the female claws. In contrast, the male of *T. trinitatis* walks backwards throughout the entire promenade. Unlike that of the scorpionids, the promenade of the buthids contains no phase in which the male pushes the female backwards. When the pair in *T. trinitatis* encounters some obstruction, the male swings round so as to change his direction and then continues his backwards progress.

There are three behaviour patterns which occur during the promenade. These are " sand-scraping ", " kissing " and " juddering ". The first two occur in *P. planicauda*, the last two certainly and possibly all three in *T. trinitatis*. There does not appear to be any special phase of the promenade when these inevitably occur and little has been found of the factors which control their appearance or absence.

SAND-SCRAPPING

This pattern has not previously been reported in descriptions of buthid courtship and has here only been definitely observed in *P. planicauda*, though there seems little doubt that, given the correct conditions, it would occur in *T. trinitatis* as well. It consists of a rapid smoothing of the soil beneath the male by the use of his two first pairs of legs. This pattern is almost the same as that of the digging which occurs in burrow excavation ; in *O. latimanus*, a scorpionid in which sandscraping has also been observed, the scraping is far slower and more reminiscent of the movements associated with removal of the soil after it has been dug free. In neither *P. planicauda* nor *O. latimanus*

does sand-scraping ever occur on hard, smooth surfaces, or soils devoid of loose sand particles. The value of the behaviour seems to be the clearing of a space suitable for the deposition of a spermatophore. Occasionally, in *P. planicauda*, sand-scraping may occur when the female is resisting the efforts of the male to pull her : the scraping is then concentrated in one spot and, as a result, the male digs into the soil. It is not clear whether this change is simply a mechanical result of the resistance offered by the female to further walking or is a definite change in the behaviour of the male : if the latter be the case, then it could be that the modified pattern is simply an elaboration of the movements of sand-scraping to permit the male to obtain better purchase with which to pull forward the reluctant female or is perhaps the true " digging " pattern, appearing as a " displacement-digging ", elicited from the male whose mating drive is thwarted by the behaviour of the female.

KISSING

This pattern consists of the male bending his pedipalps so that the mouth parts of the two animals are brought close together ; he then chews with his chelicerae at her chelicerae and pedipalp coxae. Fabre (1923) has described similar behaviour in *Buthus occitanus* Am., while Southcott (1955) has also reported it in the scorpionid *Urodacus abruptus* Poc. Both these authors suggest that the behaviour serves to stimulate one or both members of the pair. In other scorpionids which I have observed—*O. latimanus*, *O. nitidiceps* Poc., *O. austerus* Karsh and *Opisthacanthus validus* Thor.—behaviour similar to this leads to the male gripping the female's chelicerae with his own. Such a cheliceral grip has however not been observed in any buthid.

While it is possible that the " kissing " has been derived from a pattern in which the male tries to take hold of the female's chelicerae, it seems more likely that the cheliceral grip of certain scorpionids has been elaborated from the " kissing " pattern.

JUDDERING

The pattern which has just been discussed is found in both species but is far less marked in *P. planicauda* than in *T. trinitatis* ; the activity which is called " juddering " on the other hand has not been seen at all in *P. planicauda* though it has occurred in every promenade of *T. trinitatis* which I have watched. It cannot be distinguished by anything but its context from the pattern of the same name in *O. latimanus* (Alexander, 1956, 1957). A single bout of juddering consists of five to eight rapid forward and back movements of the whole body, while the feet are held still on the substratum. In *O. latimanus* juddering occurs only at the preliminary meeting ceremonies and is apparently of some importance in sex recognition. In *T. trinitatis* there may be several bouts of juddering within a single promenade and it seems possible that its main, and perhaps only, function is that of stimulating one or both members of the pair. Baerg (1954), writing of the courtship of another buthid, *Centruroides insulans* Thor., reports that the male may " shake the female backwards and forwards a few times " during the promenade ; this behaviour seems to be similar to, if not identical with, the " juddering " of *T. trinitatis*.

DEPOSITION OF THE SPERMATOPHORE

Once a suitable surface has been found and the female is in the necessary passive state, the male begins to extrude a spermatophore slowly and smoothly from his genital opening onto the substratum. Details of this structure will be given later ; it is only necessary to note here that it consists of four main parts. Distally, bent beneath the spermatophore, is the basal plate (Fig. 2a, b. pl.) which is connected by a tapering stem (s) to the capsule (c). This latter is that part of the spermatophore directly concerned with the transference of sperm. Finally, proximal to the capsule and thus the last structures to leave the genital ducts of the male, is a pair of long, slender, elastic threads, the flagella (fl).

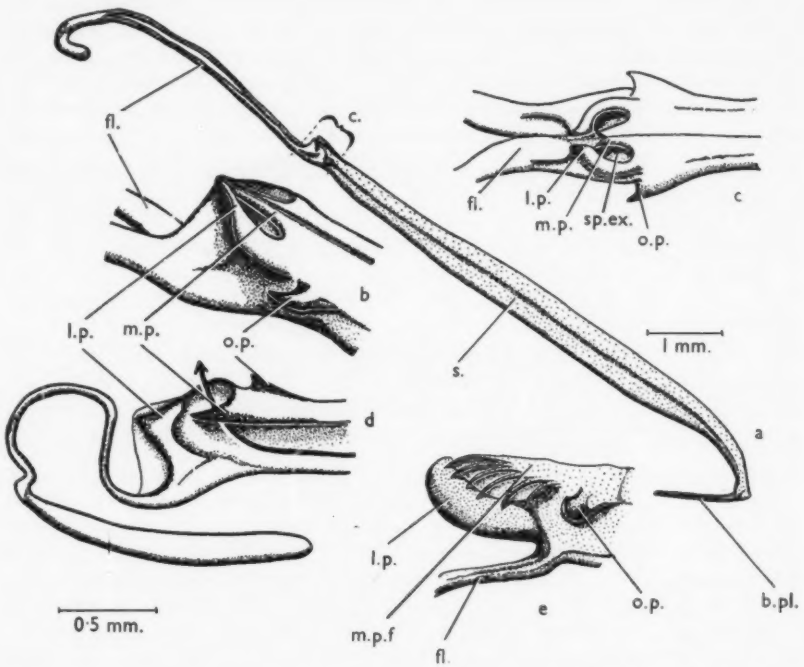

Fig. 2.—(a) *Parabuthus planicauda* : the complete spermatophore in lateral view, the distal end to the right and showing the four main parts, namely the flagella, *fl.*, the capsule *c.*, the stem *s.* and the basal plate *b.pl.* (b) the same : a dorso-lateral view of the capsular region : median process—*m.p.*, lateral process—*l.p.*, oblique process—*o.p.* (c) The same : a dorsal view of the capsule after use : paired sperm exits—*sp. ex.*, each lying between a median and a lateral process. (d) The same : the inner surface of the proximal end of a half-spermatophore. The passage of the sperm mass out of the future spermatophore is indicated by the arrow. (e) *Uroplectes triangulifer* : lateral view of capsular region showing the finger-like extensions, *m.p.f.*, on the median process.

While the spermatophore is being extruded, the male moves very slightly backward to allow the structure to emerge without being bent, and the female is, of necessity, moved slightly forward. Except for this and some limited movements of the tail of the male, the pair stand still. The whole extrusion normally takes less than two minutes, yet the spermatophore is firmly cemented onto the substratum before the next stage begins. This consists of a series of sharp backward jerks by the male, each of which pulls the female forward across the body of the spermatophore. Between succeeding jerks, the female returns to her original position : it is unclear whether this is a passive mechanical event or depends upon the activity of one or other of the pair—a thrust by the male or a retraction by the female. Normally at about the third or fourth jerk, the body of the female makes contact with the capsule of the spermatophore, so that sperm can pass into her genital ducts. This is the climax of buthid mating. The male makes no further attempts to pull the female forwards, but releases his grasp of her pedipalps and the couple break up. This climax, when the capsule of the spermatophore makes contact with the genital apparatus of the female, will be described as " hooking ". At this point of the description, it is necessary to go back and point out other slight differences between the two species which have so far been passed over.

In both species the male, when he has the freshly deposited spermatophore beneath him and has not yet jerked the female for the first time, still has the pair of flagella within his body. As he moves backward at each jerk. the flagella are almost pulled from his body but the ends still remain within him. In *P. planicauda* the female moves the spermatophore slightly back with her when she returns to her former position after "hooking" and this finally separates the spermatophore entirely from the body of the male. In *T. trinitatis*, however, the " hooking " does not pull the flagella completely free of the male and, when the pair break apart, he is still attached to the spermatophore and remains for some time in this position. This is to be contrasted with *P. planicauda* where, after " hooking ", the animals separate and go their own ways almost immediately.

At this point the male of *T. trinitatis* starts what may be termed a " post-mating display ". This lasts for about two to five minutes and consists of bouts of juddering separated by intervals of thirty seconds to one minute. After about three bouts the male normally begins to make alternating chewing movements with his chelicarae and may thus manage to damage the spermatophore to some extent, though he has never been seen to eat it, behaviour recorded by Angermann (1955) in the female scorpion *Euscorpius italicus* (Hbst.). Eventually one of his judders frees the male and he walks away.

In neither species does the female run away but normally remains for a short time after the male has released her and, in such cases, she will lower her prosoma on to the ground and, with the operculum held open, move the genital opening backwards and forwards along the soil surface. Similar behaviour has been observed in the female of *O. latimanus* (Alexander, 1957) and it seems possible that it is concerned with ensuring that the sperm penetrate deeply enough.

INFORMATION ABOUT THE SOIL SURFACE

So far it has been taken for granted that the male scorpion is capable of differentiating between a surface which is suitable for supporting a spermatophore and one on which it might collapse, but no evidence has been given for this, nor has any suggestion yet been made as to how it is done. In attempting to resolve these problems, observations made on *P. planicauda* and on scorpionid *O. latimanus* will be quoted. Where identical results have been obtained from both species no distinction will be made between them in the text.

That a male can distinguish different qualities of surface is shown by the fact that, if the soil be loose or the surface too slippery, the promenade will go on for hours, though, as soon as an " acceptable " surface is provided, the pair will mate within a few minutes. Similarly, if a patchwork of suitable and unsuitable surfaces be presented, the male will only deposit his spermatophore in one of the former areas. If he has clearly adopted the pose characteristic of spermatophore extrusion and a little loose sand is carefully introduced beneath him, he will suddenly " change his mind " about the site and move off to another. The surfaces suitable for one species are not always those particularly favoured by another: for example *O. latimanus* will accept blotting paper, rough cardboard, mud smoothed and dried to form an arena or a surface of unpolished wood; while in the laboratory *P. planicauda* has not yet been seen to mate on any surface other than a particular matt cardboard and *O. austerus* has refused all surfaces other than a close grained wood.

Thus it is clear that a differentiation is made and problem remains as to how it is done. The first suggestion comes from watching the animals as they promenade: the pectines of the male are kept unusually busy, while those of the female are almost still. It will of course be remembered that it is the male who must make the site selection and, furthermore, that in almost every species his pectines have more or longer teeth than do those of the female. These facts suggest that the pectines carry the sensory structures concerned in selection of a mating site and this point has been tested experimentally.

Both pectines of a responsive male were ligatured tightly at the base and then amputated. After a week or two he was replaced with a female and observed. In two cases out of three the male began to court the female immediately and this led on to a promenade which continued across both suitable and unsuitable surfaces until the female began to " get impatient ": she would cling to the cardboard, refusing to go on to the sand, but once on the latter she would walk quietly with the male. Although there was no sign of substratum recognition by the male, the possibility cannot be excluded that he had been made incapable of mating by the amputation and that the rest of his behaviour was also abnormal.

A second technique was used in which the pectines were merely immobilised: they were stuck to the coxae of the legs with Samsonite, a quick-drying adhesive with an acetone base. Once again the male would court but refused to mate. The bands of Samsonite were then removed from the pectines of such an animal, he was replaced with the female and mated within a few minutes. These various observations make it reasonably certain that amongst the sense organs carried on the pectines are indeed those concerned in the selection of a mating site.

THE SPERMATOPHORE

Without any stretching of the ductile flagella, the spermatophore in both *P. planicauda* and *T. trinitatis* is about 15 mm. long and 2 mm. wide. This slender structure is composed, partly at least, of chitin, partly of scleroprotein and as it emerges from the male is a creamy white tinged with pink. As it dries and hardens, it slowly darkens in colour to a deep brown. It is formed as two separate parts, a right and left. The description of the spermatophore is more comprehensible if the organisation and origin of its parts and associated glandular structures be considered at the same time. There have been several accounts of the genital organs of various buthids, the most recent being that by Abd-el-Wahab (1957) on *Buthus quinquestriatus* (H.E.). However since these accounts were prepared with no knowledge of the exact events associated with fertilisation, both the descriptions and the terminology used are at times unsatisfactory. It seems nevertheless desirable to retain as many as possible of the terms proposed by Abd-el-Wahab and where a change seems essential, the terms employed by him are given in brackets. Where the facts obtained from a study of *P. planicauda* and *T. trinitatis* suggest a reinterpretation of the structures in *B. quinquestriatus* this has been attempted.

Fig. 3a and 3b show the genital systems of *P. planicauda* and *B. quinquestriatus*. The difference in arrangement of the testes is not significant for, as Abd-el-Wahab agrees, these vary from species to species and sometimes within the same species. Similarly differences in the shape and size of the seminal vesicles and ampulla are of no importance as they alter with the amount of sperm being stored. Each spermatophore sac (ejaculatory sac) contains the cuticular skeleton of half the spermatophore, here called a half-spermatophore (supporting shaft of the ejaculatory sac). When the deposition of the spermatophore is about to begin, these half-spermatophores pass forward and into the common chamber where fusion occurs. As they pass forward a rotation takes place so that the two halves which are to be fused together become correctly orientated one to the other. Thus a point on a half-spermatophore which lies ventro-laterally in the spermatophore sac must rotate through about 100° to reach the mid-dorsal position. Once the appropriate parts of the pair of half-spermatophores are in contact, the actual junction is achieved in *T. trinitatis* by a slight overlapping of their margins, that of the right-hand side lying above the margin of the left side dorsally and beneath it ventrally. In *P. planicauda*, as in the scorpionids, the margins of the half-spermatophores meet but do not overlap significantly. There are only three regions along the margins where no fusion takes place. The first is just proximal to the basal plate, a point through which the material which cements the basal plate to the substratum emerges. The second is that part of the capsule through which the sperm passes to the female. Finally the main length of the two flagella are separate from each other except at their free ends where a large sticky lump of each tends to glue them together. The basal plate, which is bent back beneath the deposited spermatophore to support it, consists of the joined anterior ends of the half-spermatophores (anterior processes of Abd-el-Wahab).

In *Uroplectes triangulifer*, these processes are already partly fused even before the extrusion of the spermatophore begins. In *P. planicauda* and

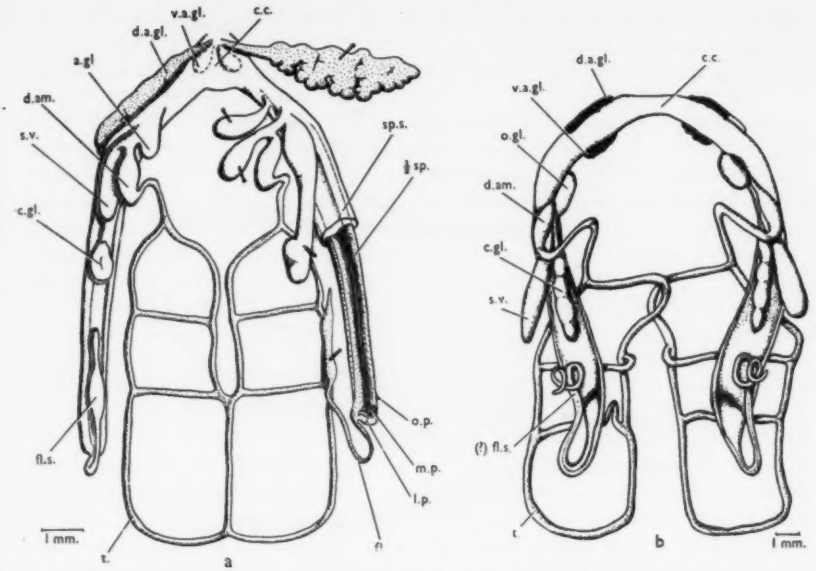

Fig. 3.—Dorsal view of the genital systems dissected out from two male buthids. (a) *Parabuthus planicauda* : half of the spermatophore sac, *sp.s.*, has been dissected away on the right side to expose the half-spermatophore, ½ *sp.*, and the three processes of the capsular region, *m.p.*, *l.p.*, and *o.p.*, while the flagellum sac, *fl.s.*, has been removed to show the flagellum, *fl*. The associated glands of the right side have been freed from the spermatophore sac : the oval gland *o.gl.*, the cylindrical gland *c.gl.*, the seminal vesicle *s.v.*, and the ampulla of the vas deferens, *d.am.* have been reflected and pinned out. The dorsal annex gland *d.a.gl.*, of the right side has been pinned forward while the two ventral annex glands *v.a.gl.*, can be seen beneath the common chamber *c.c.*, The network of the testis *t.*, is shown. (b) *Buthus quinquestriatus* : (after Abd-el-Wahab, 1957). Labelling as in Fig. 3a.

T. trinitatis however the right and left halves are quite separate initially and they only unite as they pass through the common chamber. In all cases however these processes do not " from a tabular organ for transmitting the sperms . . . into the female during the process of copulation ", the suggestion put forward by Abd-el-Wahab for the homologous parts in *B. quinquestriatus*.

On either side just anterior to the opening of the seminal vesicle into the spermatophore sac, there is a small gland, the oval gland (o. gl of Fig. 3). Immediately after mating, the oval glands are empty, as are, of course, the spermatophore sacs. At other times, however, each oval gland contains a viscous fluid which solidifies very quickly in air. The contents of each gland form the pedal wings ; similar structures have been described in the scorpionid, *O. latimanus* (Alexander, 1957). In *P. planicauda* the oval glands do not receive their contents from the ampullae of the vasa deferentia, as reported for *B. quinquestriatus* (Abd-el-Wahab, 1957), but the walls of the gland itself appear to secrete the material forming the pedal wings. Abd-el-Wahab reports that the wall of the oval gland of *B. quinquestriatus* is histologically similar to

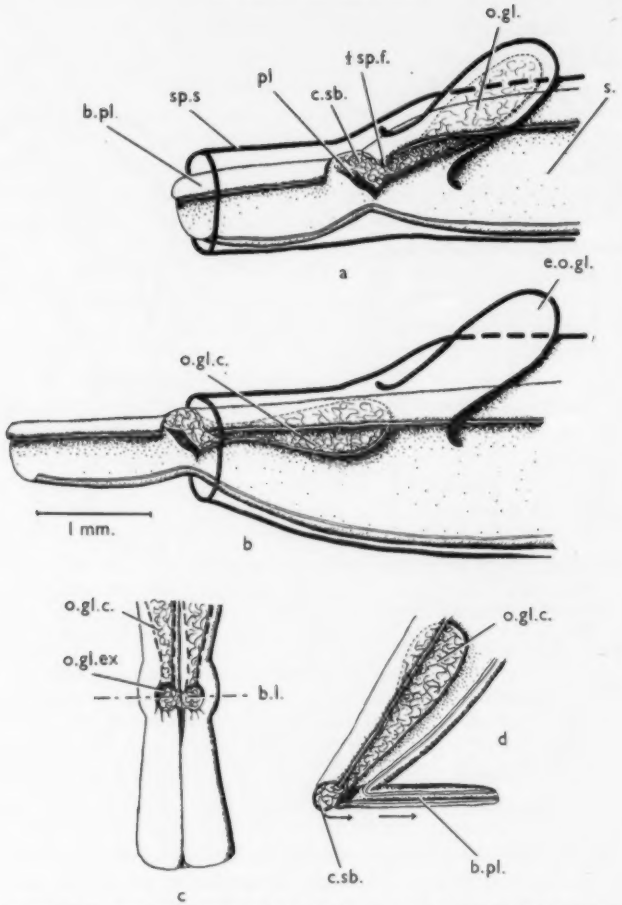

Fig. 4.—Diagrammatic representations of the distal end of a buthid half-spermatophore to show how the basal plate becomes cemented onto the substratum. (a) is a lateral view of the half-spermatophore still undisturbed within the spermatophore sac *sp.s.*, which is indicated in heavy black lines as is also the oval gland *o.gl.*, whose contents enter the lumen of the sac and abut on the plate *pl.* which prevents the fluid from flowing into the lumen of the basal plate *b.pl.* Both the basal plate and the stem *s.*, have their edges folded over except at the point *c.sb.* where the contents of the oval gland will escape when the spermatophore is extruded. The margins which will fuse with those of the left half-spermatophore can be seen as narrow white lines. In (b) the half-spermatophore is partly out of the spermatophore sac, having drawn the contents of the oval gland *o.gl.c.*, with it, leaving the oval gland empty *e.o.gl.* Due to the arrangement of the small flap ½ *sp.f.*, the secretion from the oval gland of each side is caught beneath the fold of the stem. When the two half-spermatophores fuse these two sticky masses come to lie side by side as in (c), beneath the folds which have fused to form the dorsal surface of the complete spermatophore. (c) is a dorsal view of this region and shows the

[*Continued bottom next page*]

that of another gland which is known to secrete. It thus appears possible that he has misinterpreted matters in *B. quinquestriatus* and that the material of the pedal wings is here also secreted by the walls of the oval gland and not derived from the ampullae.

Just opposite the opening of the oval gland into the spermatophore sac there arises from the half-spermatophore a small flap (Fig. 4) onto which material from the oval gland becomes attached, so that it is possible to withdraw the contents of the gland by slowly pulling the half-spermatophore from its sac (Fig. 4b). When a half-spermatophore is drawn out in this manner and its half of the basal plate bent as it would be in the natural deposition of the whole spermatophore, then the material forming the pedal wing is moved forward so that, if the basal plate were on the ground, the wing would touch the ground as well (Fig. 4d). In natural conditions the wing would then seal the basal plate onto the ground. If the wing-forming material is removed from a freshly dissected oval gland and smeared onto the ground, the material will dry within a very short time to the cement-like consistency which is typical of the substance which normally fuses the deposited spermatophore to the substratum. Thus it would appear that the function of the oval gland in the buthids is to produce a secretion which anchors the spermatophore to the ground. A pair of very similar glands occur in the scorpionids, the " glands anterieure " figured by Vachon (1949) in *Heterometrus longimanus* Herbst., and these glands have been reported to secrete material which serves the same purpose (Alexander, 1957). Bücherl (1956) suggests that the function of the oval gland secretion is that of nutrition of the sperm : there is however no evidence offered in support of this idea.

The next problem to be considered is how a junction is effected where the two margins of the spermatophore meet or overlap. It has been suggested, albeit without evidence, that two small glands entering into the common chamber are responsible for this action in the scorpionids, *O. latimanus* (Alexander, 1957) and *Heterometrus scaber* Thor. (Mathew, 1957). These two glands, one dorsal and the other ventral, are perhaps homologous with the pairs of dorsal and ventral annex glands which occur in *P. planicauda* (Fig. 3a) and *T. trinitatis* as well as *B. quinquestriatus*. Circumstantial evidence for attributing this function to these glands is their position : firstly they open into the common chamber and it is here that the half-spermatophores must be stuck together. Secondly there are both dorsal and ventral openings as would be desirable since both dorsal and ventral margins of the half-spermatophores must be sealed.

To test this hypothesis two half-spermatophores were dissected out of a freshly killed male *P. planicauda*, the margins were adjusted in the appropriate manner and some drops of secretion from the annex glands were applied to the preparation. After being left overnight, those edges of the spermatophore

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two confluent exits for the oval gland contents *o.gl.ex.* As the basal plate touches down onto the substratum, it bends along the line *b.l.* so that the condition represented in (d) is achieved. Here only one half-spermatophore is drawn so that the contents of a single oval gland, *o.gl.c.*, are shown and, from the arrows beneath the basal plate, *b.pl.*, it can be seen how the fluid flows to cement down the basal plate.

which had been touching each other were so firmly fused that the whole structure was broken during efforts to separate them. Thus it seems highly probable that it is the secretion of the annex glands which serves to stick the halves of the spermatophore together : a thesis which is also put forward by Bücherl (1956) for *T. trivittatus* and *T. bahiensis*.

So far none of the observations reported here have shown any marked difference between the spermatophore of the scorpionid, *O. latimanus* (Alexander, 1956) and that described above for the buthids. The major difference in the actual mating of the latter animals and of a scorpionid lies in the method of taking the sperm up from the spermatophore : in the buthids this is done instantaneously during " hooking ", but in *O. latimanus* the female triggers off an " explosion " of certain parts of spermatophore capsule into her body and these are held within her for about five minutes while the sperm pass through. This difference is reflected by the presence in the buthids of the cylindrical gland, absent in the scorpionids, and in the form of the capsular portions of the spermatophores. The details of the capsular region will be considered first.

The stem of the spermatophore is long and hollow, narrowing somewhat towards the capsule. This latter bears a number of " processes " which Abd-el-Wahab regarded as anchoring the " supporting shaft of the ejaculatory sac " within the " ejaculatory sac ". *P. planicauda*, *B. quinquestriatus* and *T. trinitatis* have three of these processes to each half-spermatophore, three pairs to each spermatophore (Fig. 2b, c and d) ; they will here be called the median (outer of Abd-el-Wahab) lateral (inner) and oblique pairs. The pair of median processes lie very close together along the mid-dorsal line of the spermatophore. The spaces on either side between the median and lateral process are left free and it is through these that the sperm passes. In *P. planicauda* these holes are very clear in dorsal view and appear as two round openings, *sp. ex* of Fig. 2c, but in *T. trinitatis* they are mere slits. In *U. triangulifer*, on the other hand, the sperm exits are complicated by the fact that the homologue of the median process of *P. planicauda* and *T. trinitatis* ends in a number of fine finger-like projections (Fig. 2e). In this species, the two sperm exits are fully confluent.

During mating, when the genital opening of the female is directly above the pair of apertures between the median and lateral processes, the specialised lobes at the base of her pectines (Fig. 1a) are level with the pair of oblique processes. It is here that the first contact is made during mating. The events which have been called " hooking " would seem to be as follows : the oblique processes are caught by the specialised bases of the female pectines so that, when the female jerks back to her former position, these processes are pulled back and downward towards the basal plate. Since this latter is fixed, the movement of the oblique processes has the effect of increasing the pressure within the hollow stem of the spermatophore and sperm that are lodged there are driven out through the openings at the top of the capsular region. The same mechanical forces are involved in the mating of the scorpionids, but in this case the compression set up between the capsular region and the fixed basal plate leads to the bending of the spermatophore and eversion of the valves.

The above consideration raises the question of the exact nature of the material which is found within the stem of the spermatophore. This, when examined fresh, contains sperm, large numbers of them bound together as little rods and giving off a pink irridescence in the case of the buthids I have observed, green with the scorpionids. Examination of the contents of the stem of a spermatophore which was deposited without the female " hooking " and was subseqently fixed, revealed in addition, an elongated structure, somewhat tough and probably formed from two separate parts since it was easily divided down the middle. It seemed probable that this constituted the contents of the cylindrical glands, that it might be important in transmitting the sperm to the female and could possibly even be the basis of the spermatocleutrum which is found within the vagina of the female scorpion and which is stated by Vachon (1953) to be placed there by the male.

The above suggestion makes it necessary to consider now the contents of the cylindrical glands. Abd-el-Wahab (1957) makes no mention of these structures having any inclusions in the male of *B. quinquestriatus* but Bücherl (1956) states that there is a secretion present within the cylindrical glands of the two species of *Tityus* that he was studying, though he gives no further details nor makes any suggestion as to its possible function. In the male of *P. planicauda* which is ready to mate, the glands each contain a long soft rod (*r.* of Fig. 5a), which has a sticky lump at either end (*j.m.*, Fig. 5a). This rod dilates towards its posterior end and, more especially in *T. trinitatis* (Fig. 5b) this dilation is somewhat ridged. Here the smaller of the two sticky lumps

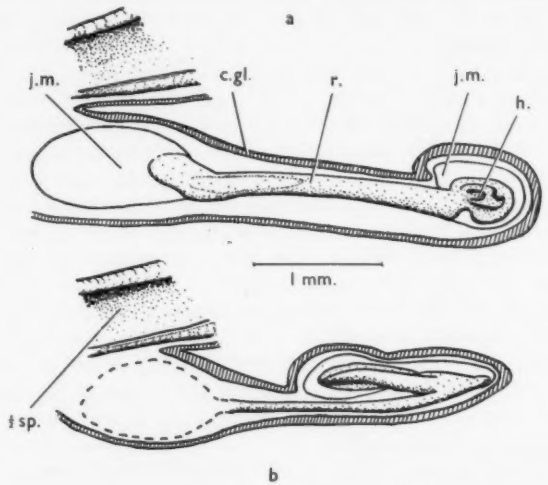

Fig. 5.—Diagrammatic representation of the contents of the cylindrical glands of two buthids, (a) *P. planicauda* and (b) *T. trinitatis*. The wall of the gland *c.gl.*, is cross-hatched while a small piece of the half-spermatophore ½*sp.*, is also shown. The contents in either case consist of a narrow rod *r.*, with a jelly mass *j.m.*, at either end, that of the posterior end being attached to the head *h.*, of the rod.

is attached. The freshly dissected rod is whitish and somewhat transparent, looking as though it were composed of minute particles set in a transparent jelly. In alcohol fixed specimens, or individuals which have been dissected under van Harreveld (1936) ringer solution and left for some hours, the rod is dark in colour and much tougher : it appears to have become sclerotised. The rod is largely protein, but gives a positive chromaffin reaction, indicating the presence of a dihydroxyphenol such as might be concerned in the tanning of a protein to give a scleroprotein. Thus the rod is soft structure which would adopt the shape of a space into which it is forced and yet harden and tan automatically. These are the properties which might be expected in the material precurser of the spermatocleutrum.

The chemical characteristics of the two jelly masses are less well defined : they are protein and, though they do harden in alcohol-preserved specimens, they do not turn brown.

If the half-spermatophore is withdrawn gently from a freshly killed male, it carries with it the contents of the oval gland, as has been described above. The contents of the cylindrical gland, however, remain *in situ*. This does not however exclude the possibility that the contents of the cylindrical glands are actively extruded into the lumen which is formed when the two half-spermatophores are fused together. Certainly there are muscle fibres in the walls of the cylindrical glands : such structures could form the basis for active extrusion of the contents of the gland. Indeed, low intensity electrical shocks to the wall of the spermatophore sac cause the extrusion of the cylindrical gland contents as well as the half-spermatophore itself. Certainly the pair of rods and their associated jelly masses are absent from the cylindrical glands of a recently mated male *P. planicauda*.

In support of what has been suggested above of the formation and functioning of the spermatophore a single further observation will be quoted. In this a male was killed and preseved while he was actually extruding a spermatophore. Fig. 6 illustrates what information could be obtained from such a specimen. At the point where the pair of annex glands open into the common chamber, the union of the two half-spermatophores begins—which is what would be expected if these two pairs of glands are concerned with joining the two half-spermatophores together. The glands themselves appear to be in the process of secretion, as may be judged from the withdrawal of secretory material from their distal ends (*d.a.gl.*). There is, however, still much material ready to be extruded, as would be expected since most of the spermatophore has still to be stuck together. The oval glands are completely empty and their contents have presumably contributed to the material at the base of the spermatophore. The apertures (*o.gl.ex.*) through which this material would have to pass to reach the substratum are clearly visible.

The cylindrical glands have already liberated their contents so that the pair of rods and their attached jelly masses (*c.gl.c.*) lie towards the base of the spermatophore stem. At the point when the animal was killed, the seminal vesicles, which are almost full, must have just begun to pass their sperm masses into the lumen of the stem, for there is a small patch visible (*sp.*).

To allow the half-spermatophores to pass out, the spermatophore sacs are

contracted so that they, and the cylindrical glands appear shrivelled, with marked transverse folds showing across them (*sp.s.f.* and *c.gl.f.*). As Mathew (1957) suggests, it was probably a male scorpion with genital organs in this condition that Pavlovsky saw and described (1917) as an abnormality.

The only structure whose function cannot yet be satisfactorily recognised, is the contents of the cylindrical gland. It was tentatively suggested earlier that the rods might be transferred with the sperm into the female and there form the basis of the spermatocleutrum. There are however objections to such a view. Firstly that the rods within the spermatophore stem are so far from the sperm exits (see Fig. 6) ; secondly that, once they are together within the stem, there seems little possibility of the rods separating to pass out from the two separate sperm exits and, lastly, that the scorpionids, though they have no cylindrical glands, still produce spermatocleutra.*

It therefore seems reasonable to look at the matter in another light, and, to begin with, it is necessary to consider the form of the spermatophore. There are clearly some advantages in the spermatophore stem being fairly long—it facilitates the orientation of the female genital aperture to the capsule and it seems almost a necessity if the pair are to be " at arms-length " as occurs in the Buthidae (see p. 156). A long, hollow stem would however present an immediate difficulty, for the enclosed sperm would tend to flow down it and away from the sperm exits. The obvious resolution of this difficulty would be to make the stem solid, a condition found both in some mites (Byers, *et al.* 1957) and in at least some pseudoscorpions (Vachon, 1938). In both these cases however the stem is very slender and, while this arrangement is possible for such small animals as mites and pseudoscorpions, it might well prove impractical for larger animals such as the scorpions. With a larger spermatophore a solid stem would clearly be wasteful of material while problems of hardening within a short time might also arise. A transverse septum could however prevent the downward flow of the sperm mass. The reason why such a solution has not been adopted in the case of the buthids will be clear later ; but a similar principle has been adopted by the scorpionids, where there are present a pair of small catching devices, the sacculi, within the capsular region (Alexander, 1957). The success of this device is however intimately bound up with the whole mechanism of " explosion " which has been evolved in this group.

The other possible solution to the problem would be to secrete a separate " filling-agent " which could be pushed down into the lumen of the stem to block it up. The Buthidae seems to have exploited this possibility : the

*Three female scorpionids were killed within fifteen minutes of mating and in none of these were there any signs of the normal spermatocleutrum though one of these animals had a structure lying at the base of the common vagina and this was almost certainly a newly formed spermatocleutrum with the lines of sclerotisation very indistinct. This together with the fact that no structure resembling a spermatocleutrum has ever been found in an opened spermatophore, leads to the suspicion that it is formed by the solidification of some secretion within the ducts of the female, possibly produced by a female gland. This is supported by the findings of Bücherl (1956) who reports that the spermatocleutrum in *T. trivittatus* and *T. bahiensis* is a female secretion which reforms some weeks after a parturition, regardless of whether there has been a second mating or not.

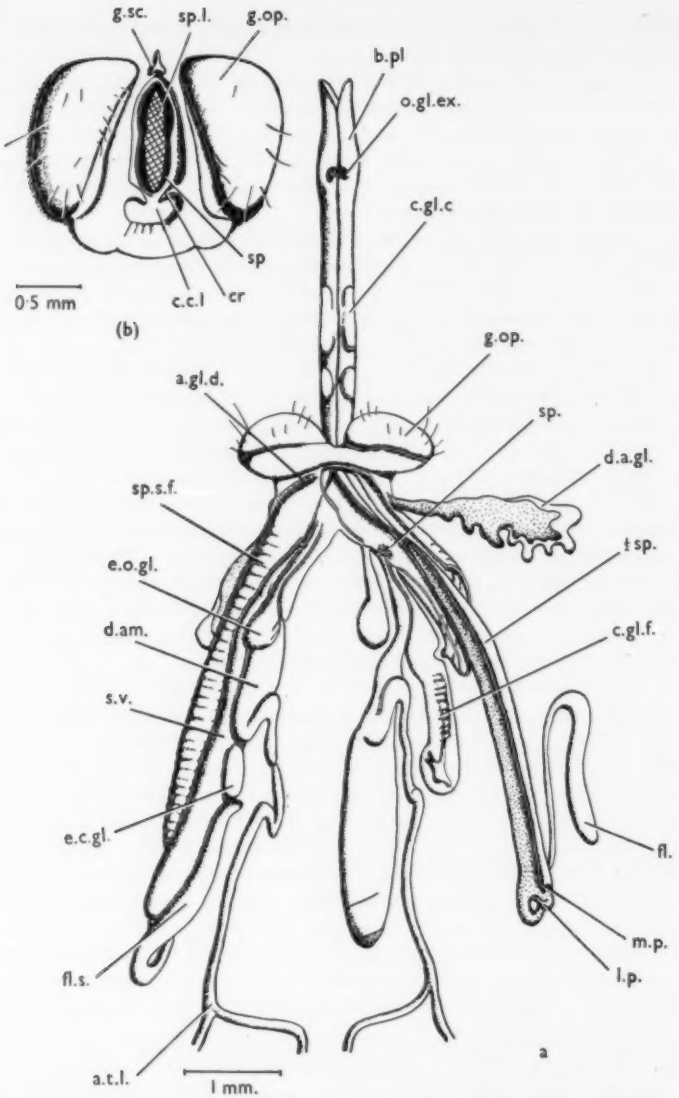

Fig. 6.—Illustrations of the results obtained by killing and preserving a male buthid as he was extruding a spermatophore. (a) Dorsal view of a dissection of the genital organs of the animal concerned. Part of the spermatophore is already extruded from between the two plates of the genital operculum *g.op.* The basal plate has not yet been folded under the spermatophore and the apertures through which the oval gland contents escape are shown, *o.gl.ex.* In the stem the position of the contents of the cylindrical glands can be seen

[*Continued bottom next page*]

rods and jelly from the cylindrical glands prevent the sperm mass from travelling down the stem towards the basal plate, and keep it near the sperm exits.

There is however one more factor to be taken into account here, namely the mechanics of sperm transfer. Up to this point in the discussion it has been assumed that, at the moment of mating, the specialised bases of the female pectines make contact with the oblique processes of the spermatophore capsule so that pressure within the stem is increased and consequently the sperm are forced out of the sperm exits and into the female. This, as far as it goes, appears to be plausible and indeed can be verified experimentally : a freshly deposited spermatophore which has not been touched by the female is used, the pair of oblique processes, or in fact even one of them, is pressed very slightly down in the direction of the basal plate, and two streams of sperm are immediately shot out of the sperm exits. Nevertheless, a recognition of how the rods and jelly masses participate in this phenomenon allows a fuller comprehension of its efficiency. The distal jelly masses will block the opening through which the oval gland contents escaped to the substratum and so keep both the rods and sperm mass in place. The proximal mass of jelly will keep the sperm within the capsular region where it is required. The pair of rods, as has been explained earlier, harden quite rapidly and, soon after the extrusion of the spermatophore, should be capable of acting in the manner of a plunger within the tube of a syringe. In normal use the plunger is pressed into the tube, thus squirting out its contents : here the plunger, in the form of the pair of rods, is not moved directly, but the tube, that is the stem of the spermatophore, is pushed down towards the basal plate by the pressure of the female pectinal specialisations, to that the sperm are squirted out of the sperm exits and into the female opening which is directly above them.

At this point it is possible to see that this system offers advantages over a simple septum as a device for retaining the sperm mass in position within the spermatophore stem, for the two rods, derived from the cylindrical glands, force the sperm out of the spermatophore, a process which could not easily be effected by a simple septum.

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c.c.gl. The spermatophore sacs which have been dissected out of the body are strongly contracted, as can be seen by comparing their lengths here with that in Fig. 3a relative to the anterior loop of the testis *a.l.t.* This contraction is reflected in the folds shown on the spermatophore sac *sp.s.f.* and the cylindrical gland *c.c.gl.* Both the oval glands and the cyclindrical glands *e.o.gl.* and ampulla of the vas deferens *d.am.*, are still full of sperm, the first of which to leave the sperm duct can be seen on the right-hand side, *sp.*, where the spermatophore sac has been removed to show the half-spermatophore within, the manner in which this has to be twisted to join with its fellow of the other side. The dorsal annex gland *d.a.gl.*, of the right side has been freed from the spermatophore sac and it can be seen that the distal end of the gland lacks secretory matter which has presumably passed out into the lumen of the common chamber. The duct of the left dorsal annex gland *a.gl.d.*, has been exposed. (b) View of the external genital area of the animal. The spermatophore has been broken off close to the point at which it emerges from the body. The two plates of the genital operculum *g.op.*, have moved apart, and the lumen of the common chamber *c.c.l.*, can thus be seen. In it is the portion of the spermatophore *sp.*, with its lumen full of sperm *sp.l.* The pair of crochets, *cr.*, seem to play some part in guiding the spermatophore out, as may be judged from their position in this specimen. A small genital sclerite—*g.sc.* is present.

DISCUSSION

In the buthids it is invariably the male scorpion who begins the courtship and, indeed, since the part of a responsive female seems to be that of passivity throughout, it could hardly be otherwise. Two questions may be asked :— " What stimulates the male to start courting ? " and " how does he distinguish a female from another male ? " On neither of these points is there as yet any satisfactory evidence. Observations made on *P. planicauda* at different times of the year suggest the existence of a preferred breeding season, in so far as males will mate less readily during the winter. Comparable observations on *T. trinitatis* could not be made. Further, from casual observations, the impression is gained of a fluctuation in both species of any one male's sexual drive from day to day. Crane (1949) has shown, using models, that such a phenomenon is found amongst male salticid spiders so that its occurrence in scorpions would not be surprising. However, until a satisfactory method of measuring the sex drive of the male has been devised, there is little point in considering what factors could control either the seasonal or day to day fluctuations.

As far as sexual recognition is concerned, it will be remembered that in *T. trinitatis* there is a marked sexual dimorphism in both size and colouration of the tail, while at the initial meeting of the two sexes the male grasps preferentially at the female's tail. This suggests that the differences in shape and colouration of the tail in the two sexes may be an important element in sex recognition.

Whether, in *T. trinitatis*, there are other releasers eliciting courtship from the male, is not known. In *O. latimanus* the primary releaser appears to be a behavioural difference in response to the juddering of the approaching male (Alexander, 1957), but I have also evidence, as yet unpublished, for a reaction to the smell of a responsive female so that clearly scent could also be one of the initial releasers : this point was not tested in *T. trinitatis*.

As was remarked earlier, there is no indication of how sex recognition is done by the male of *P. planicauda*. It seems that the animals must get very close together before they can determine each other's sex and it is tentatively suggested that in this species sexual recognition depends solely upon the ability of the female to emit a distinctive odour which can be recognised by the male. Certainly *P. planicauda* is able to react to smells.

Arbre Droit

It may be noticed in passing that neither of the buthids whose courtship is described here show any sign of the classical arbre droit as part of the introductory ceremonies of mating. This is in accord with observations on *B.* (= *Leiurus*) *quinquestriatus* in which Thornton (1956) could find no arbre droit. Baerg (1954), also writing of a buthid, *Centruroides insulans* Thor., remarks that the tails of both animals are up and that the male does occasionally stroke the back of the female. This is however during the promenade and thus not strictly comparable with the behaviour described by Fabre (1923) in *B. occitanus*. Indeed the arbre droit does not seem to have been recorded as an integral part of courtship by any recent observers of scorpion mating. I have

previously reported (Alexander, 1957) that the only pattern in *O. latimanus* resembling an arbre droit is when a male is attempting to court an unreceptive female. It seems possible that this pattern, seen indeed by Fabre on only one occasion between two apparently responsive members of opposite sexes is not a normal component of scorpion mating at all.

Juddering

As has been mentioned above, the juddering which occurs in *T. trinitatis* appears to be identical with that described for the scorpionid, *O. latimanus* (Alexander, 1957) : the only difference which is apparent is that the former occurs during the promenade when the male has hold of both pedipalps of the female and the latter during the introductory ceremony before any grasp has been established. The probable function of both has already been discussed and it is only their evolutionary origin that is considered here. From the rate and the violence with which the male of *T. trinitatis* jerks the female over the spermatophore during the actual mating, it might well be that this pattern is the one from which the juddering is evolved. On the other hand it is possible that its derivation is the same as that suggested for the juddering in *O. latimanus*, namely an investigatory pattern in which the body and more especially the pedipalps are thrown forward and backward. There is no reason why the two should not have evolved thus separately ; indeed the difference in the context in which the behaviour appears would possibly lead one to expect separate derivations, that in *O. latimanus* arising autochthonously from a situation where investigatory behaviour is called for, that in *T. trinitatis*, and perhaps in *C. insulans* as well, arising, also autochthonously, from a mating movement as the intensity of the sexual drive becomes higher. A possible point of support for this interpretation of the judder of *T. trinitatis* is the fact that it is not yet clear whether the movements that Baerg saw in his Jamaican scorpions were really juddering or actually those of mating itself.

This sort of difficulty underlines very clearly one of the limitations inherent in analysing behavioural observations in terms of modern ethology. All suggestions of the origin of derived movements are of necessity speculative and not open to experimental investigation, though the close study of related species may add further circumstantial evidence.

Post-mating display

This phenomenon, which does not seem to have been observed in any other invertebrate, raises two questions : namely " what is the functional significance of the display in *T. trinitatis* ? " and " how did this pattern arise ? "

Post-copulatory displays occur in some birds and fishes. The simplest theory concerning the evolutionary significance of this type of display has been put forward by Lorenz (personal cummunication) in relation to geese. He suggests that the display serves to keep the pair together at a time when the mating drive has sunk to its lowest ebb and aggressive tendencies, previously masked by sexual activities, will be freed : as a consequence of this the pair may break up with unfortunate results to the coming young. In scorpions too the rôle of this display might be that of suppressing the aggression

which certainly does arise in the female immediately after mating. The advantage of this, however, would not be in preserving the pair, since pair formation does not occur in these animals, but in preventing the female from killing the male after she has mated—a phenomenon which has frequently been reported among the Arachnida. If this were correct then one would expect to find either that post-mating display is shown in all species or that the female of *T. trinitatis* is particularly aggressive and thus requires special treatment by her partner. Neither of these is true however, and a slightly different hypothesis is therefore put forward here, although it is freely admitted that it is based on only the most tenuous evidence.

This hypothesis depends on three facts :—(a) the female is always more aggressive immediately after mating and should therefore be avoided by any male : (b) male scorpions will normally have more sexual excitation than will be " used up " during a simple uncomplicated mating and there is, consequently, a danger that, if the female stimulates the male to begin courtship again, she may then attack and perhaps kill him ; (c) it has been suggested above that in the initial stages of courtship the male of *T. trinitatis* responds not to a specific behaviour pattern performed, nor to a specific smell emitted by the receptive female, but to her anatomical characteristics. These cannot, as a result of mating, alter in such a way to render her no longer " attractive ". It is therefore suggested that a post-mating display is incorporated in the mating pattern of this species to keep the male " occupied " and thus unable to resume courtship of the female who is now aggressive though still attractive. Thus the function of the male display may be to prevent the male being killed by the female, but the suggestion is that this protection is achieved not by suppression of the aggressive tendencies of the female, but by keeping the male out of harm's way.

The first of the above points is very easily seen in the fact that the rebuff given to a courting male by a non-responsive female is nothing like as vicious as the aggression of a freshly mated female scorpion. It is also recognised in other animals and is indeed, half of the basis of Lorenz's argument for the " pair-retaining " function of the post-mating display.

The second fact, that a male is willing to return to courtship *immediately* after mating, has been frequently observed in the scorpions and is especially clearly shown by *O. latimanus*. Such behaviour may seem surprising ; teleologically in so far as it exposes the male to the danger of death or mutilation, physiologically in so far as the male is unable to mate again successfully until a new spermatophore has been formed, a process taking about three weeks. Whether the courting drive of the male falls off in intensity during the days after mating, has yet to be investigated. The functional significance of this continued high courting-drive in the male may depend on the fact that it is difficult to orient the female correctly onto the spermatophore. Thus the mating-jerks may have to be continued over a period varying from a few seconds up to fifteen minutes. With the close relationship between the mating-jerks and general introductory courtship, it may be impossible to separate the two and to select for rapid fall of courtship activity in an animal in which the actual mating-jerk drive must be kept high.

The last point on which this hypothesis rests is the most uncertain as it has yet to be shown experimentally that sexual recognition in *T. trinitatis* is indeed dependent upon the anatomical differences between the sexes. If this point is, however, provisionally conceded the idea is itself valid within the bounds of our present knowledge. Thus in *O. latimanus* sexual recognition depends upon behavioural responses and in *P. planicauda* probably on smell. In both cases the mated female appears to loose all attraction immediately after insemination. Clearly both these methods of sexual recognition are based upon factors which are far more mutable than an unconcealable anatomical characteristic and can be rapidly changed so as no longer to release a courting pattern from the male.

It was at this stage of the speculation relating to the function of the post-mating display of *T. trinitatis* that an observation was made of a courtship which ended in mating in the buthid *Uroplectes triangulifer*. This fully supports the hypothesis erected above and for this reason the events in *U. triangulifer* are described briefly, though it must be held in mind that only a single observation has been made of the complete mating sequence of this scorpion.

As in *T. trinitatis*, there is a strong sexual dimorphism shown in the length and colouration of the tail. In the courtship the observer can see very clearly that it is the female's tail to which the male is attracted for he grasps at it continually and only after quite some time does he eventually take her by the pedipalps. During the promenade, as *P. planicauda*, the male holds the female by one of her pedipalps and walks in the direction in which he is facing rather than backwards as does the male *T. trinitatis*. There were slight indications of the " kissing " pattern but neither the sand-scraping nor any juddering ocurred during the promenade. The absence of the former may simply have been that the pair were on suitable ground to begin with. Before the male had actually taken hold of the female there were very slight indications of a possible judder in that, as he got excited by a female walking away from him, the male would stop and give a single jerk of his body and pedipalps. There was never any sign that this behaviour might be used in recognition of the sexes as it may be in the scorpionid *O. latimanus*, for it was never shown between two males.

The actual mating seems to be very like that of *T. trinitatis* and the flagella were not pulled out of the male's body by the female's contact with the spermatophore. In this case it could be seen, far more clearly than in *T. trinitatis*, that it is the female who takes the initiative in breaking up the pair ; she freed herself from the male and walked away. For just over three minutes after this the male stood in the same stop, with the spermatophore still partly within him, and made single, slight jerking movements at intervals totally ignoring the female who passed very close to him during this stage. A few seconds after he had broken free from the spermatophore and had stopped his " post-mating display ", he did indeed make some attempt to catch hold of a female but when tested again after twenty minutes, did not appear to be excited.

Thus, while it must be remembered that the events described above have only been witnessed on one occasion, it is clear that behaviour in *U. triangulifer*, is almost exactly what could be expected if the hypothesis relating to *T. trinitatis* and its post-mating display were correct. The sexual dimorphism is present and seems to be an important sign stimulus for the courtship of the male. There is a post-mating display and this is apparently effective in preventing the male from making fresh advances to the recently mated female.

This similarity in the behaviour of *Uroplectes* and *Tityus* contrasted with that of *Parabuthus* is possibly more striking in so far as *Tityus* is assigned to one subfamily of the Buthidae (Vachon, 1949) while *Uroplectes* and *Parabuthus* are united together in another, the Buthinae.

Co-ordination between the partners during mating

The question raised here is " how does the male ' know ' when to stop trying to pull the female over the spermatophore ? " or " how can he tell that ' hooking ' has taken place ? " In the scorpionid *O. latimanus* this appears to be relatively simple : during the explosion, the spermatophore is permanently bent and this takes it out from under the body of the male so that it no longer touches the ventral surface of his body (Alexander, 1957). The same principle seems to operate in the case of *P. planicauda* for it is only when the spermatophore is " hooked " that the flagella are pulled out of the body of the male and, as soon as this is done, he releases the female. The possible adaptive significance of the long flagella, in contrast to the stalk that is used by *O. latimanus* is thus obvious : it compensates for the fact that there is a greater distance between the two animals since they are using a pedipalpar and not a cheliceral grasp.

In *T. trinitatis* and *U. triangulifer*, however, the spermatophore itself does not give the male the clue as to when he should stop his jerking, for it only becomes free at the end of the post-mating display. It would appear to be the female herself who breaks away and not the male who releases her. Here therefore the flagella do not have the same adaptive significance as in *P. planicauda*.

Although the flagella of the spermatophore of *T. trinitatis* and *U. triangulifer* are not withdrawn from the genital apperture after " hooking " they clearly have a rather similar rôle to those of *P. planicauda*. The behaviour of the male is, within limits, modified by this difference ; when the female breaks away the jerking movements of the male are replaced by juddering. The evolution of this condition could be visualised in the following way, with the initial assumption that the flagella of the spermatophore became modified in some manner—possibly in length or in elasticity—so that they could not be withdrawn upon " hooking ". As a result the male no longer recognised that insemination had been successful and the initiative of breaking away passed to the female. Once this condition had been achieved, the danger of the male making a fresh approach to the female immediately after insemination is greatly reduced, and any elaboration of his behaviour from a mere continuation of the jerking movements to a ritualised intermittent juddering will reduce it

still further. As evolution along this line proceeds, the need for the male courtship advance to be released by any specific behaviour or smell becomes less. A situation in which a male whose sexual drive is active will attempt to court any female, provided he is not otherwise occupied, may be advantageous, since it may be that his advances have some effect in increasing her sexual drive. In these circumstances a female whose drive is subliminal will be induced to mate, whereas if the advance of the male were conditional upon some releaser which she provides only when fully aroused, the encounter would not result in mating. We may thus expect that elaboration of the male post-mating display will proceed *pari passu* with a reduction in the specific releasers provided by a receptive female. At the same time it is desirable that the male should be able to differentiate between a female, whom it may be always " worthwhile " to attempt to court, and a male whom this may lead only to a fight. The anatomical differences in the male and female tails provided a basis for this differentiation, and its evolution may therefore have followed the reduction in importance of releasers provided by a receptive female.

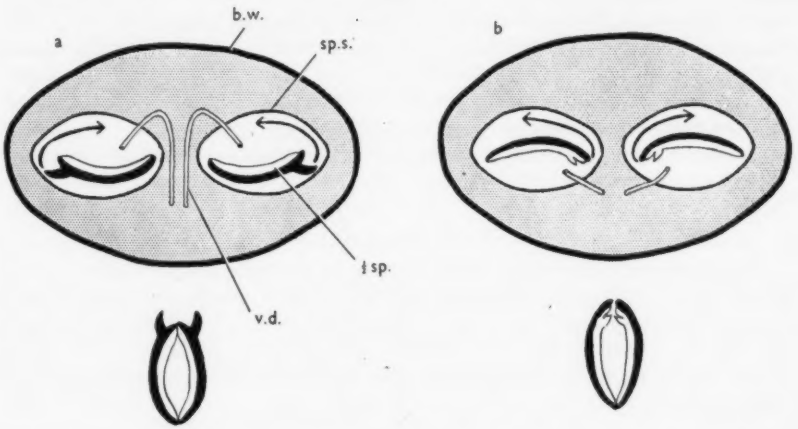

Fig. 7.—Diagrammatic representation illustrating the rotation necessary for the half-spermatophores in (a) the Buthidae and (b) the Scorpionidae, before these structures can unite to form spermatophores. The two upper diagrams represent transverse sections through the mesasoma of *P. planicauda* and *O. latimanus*, the heavy line, *b.w.*, indicating the body wall and the two pairs of thinner oval shapes within these, the spermatophore sacs, *sp.s.* Within these sacs the sections of the half-spermatophores can be seen, ½*sp.*, each being divided into two parts, the thick black part, which is ventral in (a) and dorsal in (b), is the outside of the future spermatophore, as can be seen from the two small drawings below. The clear part of each half-spermatophore forms the " core " of the completed spermatophore. The part which will become dorsal in the spermatophore is slightly lobed in both (a) and (b), the lobes in the former being lateral and external and in the latter being mesial and internal. The arrows shown within the spermatophore sacs indicate the direction in which the half-spermatophores must rotate to fuse as shown in the small drawings beneath.

Evolution of the spermatophore within the scorpionids and buthids

Although the details of the anatomy and method of functioning are different in the spermatophore of scorpionid and buthid, there appears to be a basic similarity. Thus, though the basal plate folds the opposite way in the two and the details of its formation are different, in both the anterior parts of the spermatophore are fused together to form a base while a pair of lateral glands produces a cement. Details of insemination are different but both rely fundamentally on the female pulling a pair of hooks on the capsule down towards the basal plate. It is thus of interest to notice that in both *O. latimanus* and *P. planicauda* there is a rotation of the half-spermatophores necessary before they can fuse to form the spermatophore and that in the two cases the rotation is of opposite sign (Fig. 7). Reflecting this difference are the positions of the half-spermatophore sacs, their glands and ducts which are relatively reversed in the two families : the part which will form the core of the spermatophore initially faces dorsally in the buthids and ventrally in the scorpionids. This very marked difference in anatomical relations might well be interpreted as implying that the spermatophore of the buthids and scorpionids have been independently evolved and that their similarities are convergent. However the similarities appear too great to make such an hypothesis plausible and it seems more probable that the two families have diverged from a spermatophore-bearing-stock in which the cores of the spermatophore stood vertically within their sacs and there was no rotation of the half-spermatophore during extrusion. Clearly it would be of the greatest interest to know the details of spermatophore formation in other families of scorpions and possibly such information might throw light upon the functional advantage gained by the rotation of the half-spermatophore, a point which, at the moment, remains obscure.

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SUMMARY

1. The courtship and mating of two species of buthids is described, *Parabuthus planicauda* and *Tityus trinitatis*, and the difference between these two, and between these and the scorpionid, *Opisthophthalmus*, is pointed out. In all three animals however, the mating consists of the male depositing a spermatophore on the substratum and the female picking up the sperm from it.

2. The functional anatomy of the genital organs and spermatophore of *P. planicauda* is described.

3. Points which arise out of the description of the courtship and mating as a whole are discussed, amongst them the probable releasers involved in initiating the courtship, the manner in which the male scorpion determines

whether the surface on which he is courting is suitable for the deposition of a spermatophore or not and the probable function and evolutionary origin of a male pattern called " juddering " which takes place during the promenade à deux.

4. A post-mating display which occurs in *T. trinitatis* is analysed as far as possible and a suggestion made as to its evaluation in terms of selective advantage. A single observation of mating in *Uroplectes triangulifer*, another buthid, supports the hypothesis erected for *T. trinitatis*.

5. The question of co-operation of the pair during mating is discussed. A suggestion is put forward as to how, in *T. trinitatis*, the change in the releaser values of components of the situation during mating may be linked with the evolution of the post-mating-display.

6. Lastly a difficulty, which could perhaps prove to be basic, in homologising the spermatophore of the buthids with that of the scorpionids is pointed out.

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